

A cladistic analysis of Sciomyzidae Fallén (Diptera)

Luciane Marinoni and Wayne N. Mathis

(LM) Department of Zoology, Universidade Federal do Paraná, Caixa Postal 19020, 81531-990, Curitiba, Paraná, Brazil;

(WNM) Department of Entomology, NHB 169, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

Abstract.—A preliminary cladistic analysis of adult characters is presented that illustrates the phylogenetic relationships among the genera of the family Sciomyzidae. The monophyly of Sciomyzidae is based primarily on larval characters: the habit of malacophagy and the presence of a serrate ventral arch that articulates with the lower margin of the mouth hooks. A reduction in the number of spermathecae, from three to two, is also likely to be a synapomorphy for Sciomyzidae. The analysis was done using Hennig86, and 37 morphological characters were arranged among 50 genera. After using successive weighting, six cladograms were produced, and from these a consensus cladogram was obtained. The subfamilies Salticellinae and Sciomyzinae are confirmed to be monophyletic, as are the tribes Sciomyzini and Tetanocerini. *Eutrichomelina* Steyskal, which has been placed in the tribe Sciomyzini, is transferred to the tribe Tetanocerini. The genus *Antichaeta* Haliday is confirmed to be in the tribe Tetanocerini. Illustrations of antenna and male terminalia are presented.

Among families of Acalyptrate Diptera, the Sciomyzidae Fallén (1820), more commonly known as marsh or snail-killing flies, are comparatively well studied, especially the biology of their immature stages (Berg & Knutson 1978, Ferrar 1987, Knutson 1987, Rozkošný 1997). Sciomyzid larvae are primarily parasitoids or predators on aquatic or terrestrial mollusks. This feeding proclivity may be of considerable importance to the biological control of certain parasitic, mostly tropical diseases, such as fascioliasis and schistosomiasis (Knutson 1976). The trematodes causing both diseases parasitize many of the same aquatic mollusks, as intermediate hosts, that are also fed upon by sciomyzid larvae.

Although the natural history and ecology and to a degree the descriptive taxonomy and cytology (Boyes et al. 1972) of the Sciomyzidae are relatively well known, no cladistic analysis at the generic level is available. As a step toward filling that void

in our knowledge, this cladistic study was undertaken and is reported here. To provide perspective, we begin this report with a brief overview of the higher-level classification.

In the first comprehensive treatment of Palearctic Sciomyzidae, Hendel (1900) divided the family into two subfamilies: Sciomyzinae and Tetanocerinae. Hendel characterized these subfamilies by the proepisternal seta (present in Sciomyzinae, absent in Tetanocerinae) and the frontal vitta (well developed and shiny in most Tetanocerinae, absent or reduced in most Sciomyzinae).

Cresson (1920), in a study limited to the Nearctic fauna of Sciomyzidae, recognized Sciomyzinae, as characterized by Hendel, and described two additional subfamilies: Dryomyzinae and Euthycerinae. Cresson also proposed five tribes that were divided among two of the subfamilies as follows: (1) Sciomyzinae with Oidematopsini and Sciomyzini; and (2) Euthycerinae with

Chaetomacerini, Euthycerini, and Sepedontini.

Hendel (1924) published a key to the Palearctic genera and distinguished the genus *Tetanura* Fallén as a separate subfamily, Tetanurinae, based on the following combination of characters: arista subapical, forefemur bare, and ovipositor telescoped. In the same paper and within the subfamily Tetanocerinae, Hendel also proposed the tribe Salticellini for the genus *Salticella* Robineau-Desvoidy.

Over 30 years ago, Steyskal (1965) proposed a classification for the Sciomyzidae that has been the most extensive treatment for the family from the standpoint of higher categories. Steyskal's classification, which has been adopted by most subsequent workers (Knutson et al. 1976, Barnes 1979, Rozkošný & Elberg 1984, Knutson 1987, Barnes & Knutson 1989, McAlpine 1989), recognized five subfamilies: Huttoninae, Salticellinae, Helosciomyzinae, Phaeomyiinae, and Sciomyzinae. The subfamily Sciomyzinae included two tribes, Sciomyzini and Tetanocerini. Although Steyskal's characterization of Sciomyzidae did not identify apomorphic characters, he distinguished the family from related families by the following set of morphological characters: costal vein (C) without breaks; subcostal vein (Sc) complete, free from vein R_1 ; vein A_1 complete; oral vibrissae absent; postvertical setae divergent to parallel; midfemur bearing a seta on the anterior surface; and at least one tibia with a preapical seta (Knutson 1987, McAlpine 1989). The tribes Tetanocerini and Sciomyzini are distinguished by the presence (Sciomyzini) or absence (Tetanocerini) of a proepisternal seta.

Griffiths (1972), who incorporated many characters of the male genitalia in his higher level phylogenetic study, introduced the prefamily as a category between the superfamily and the family categories. Using this classificatory structure, the prefamily Sciomyzoinea comprises the families Coelopiidae, Phaeomyiidae, Dryomyzidae, Sciomyzidae, Helosciomyzidae, Ropalomeridae,

Sepsidae, Megamerinidae, and Cremifaniidae. Griffiths' studies of Sciomyzidae were based on the following species: *Pherbellia quadrata* Steyskal, *Pherbellia griseola* (Fallén), *Sciomyza simplex* Fallén, *Pteromicra apicata* (Loew), *Elgiva sundewalli* Kloet & Hincks, and *Tetanocera robusta* (Loew). The family Sciomyzidae, as characterized by Griffiths (1972), includes Salticellinae + Sciomyzinae, and the family's monophyly is based primarily on the malacophagous habits of the larvae and the presence of a ventral arch in the cephalopharyngeal skeleton (Knutson et al. 1970, Barnes 1981, McAlpine 1989). The reduced number of spermathecae, from three to two, is likely to be another synapomorphy for the Sciomyzidae, although in Salticellinae, the number of spermathecae is four. We interpret the latter condition to be secondarily derived from two and to be an autapomorphy for the subfamily Salticellinae.

The subfamily Salticellinae has three species in two genera, the extant *Salticella* Robineau-Desvoidy and the fossil *Prosalticella* Hennig. The Sciomyzinae, which include 505 recent species, have 57, mostly widespread genera.

The purpose of this paper is to present a classification for the genera of Sciomyzidae sensu Griffiths that is based on a cladistic analysis of primarily morphological characters. Our analysis is intended more specifically to test the hypotheses that the subfamilies Salticellinae and Sciomyzinae and, within the latter subfamily, the tribes Sciomyzini and Tetanocerini are monophyletic.

Material and Methods

Fifty of the 57 genera belonging to the Salticellinae and Sciomyzinae were examined and analyzed (Appendix 1). The seven genera not examined are: *Ditaeniella* Sack, *Eulimnia* Tonnoir & Malloch, *Neodictya* Elberg, *Oligolimnia* Mayer, *Pseudomelina* Malloch, *Tetanoptera* Verbeke, and *Verbekaria* Knutson. We also studied a new genus and species from India, *Steyskalina picta*

Ghorpadé & Marinoni, that was recently described (Ghorpadé et al. 1999). Since it was virtually impossible to examine all species of each genus and suspecting that some genera may be polyphyletic (e.g., *Pherbellia* Robineau-Desvoidy with 81 species; *Sepedon* Latreille with 75 species; and *Tetanocera* Duméril with 49 species) the analysis was done with the type species serving as exemplars of each genus. The type species are always linked to the appropriate generic name.

Pelidnoptera, represented by *P. fuscipennis* (Meigen 1830), was used as the outgroup. This genus, which is in the family Phaeomyiidae (Griffiths 1972), was selected because it is morphologically similar and closely related, perhaps the sister group (Steyskal 1965, included it as a subfamily) of the Sciomyzidae. Its characters are directly comparable to those of Sciomyzidae. The family Helosciomyzidae (Griffiths 1972), represented by *Helosciomyza aliena* Malloch (1928); *Huttonina abrupta* Tonnoir & Malloch (1928); *Huttonina furcata* Tonnoir & Malloch (1928), and *Huttonina scutellaris* Tonnoir & Malloch (1928), was studied to further confirm the polarization of characters.

A matrix with 37 morphological characters of adults and one of the larval morphology was produced (Table 1). Autapomorphies for particular genera were not included in the analysis.

Multistate characters in the analysis were first treated as unordered (Carvalho 1989, Pape 1992, Marinoni & Carvalho 1993). The ordination of the characters was done in accordance with standard procedures for cladistic analysis (Wiley 1981). The polarization was done using the outgroup comparison (Watrous & Wheeler 1981, Wiley 1981, Brooks 1989).

The analysis was facilitated with the computer program Hennig86, version 1.5 (Farris 1988). To find cladograms supported by the most consistent characters, the following command sequence was used: "mhennig" (mh), "branch and swapping"

(*) and "successive weighting" (xs w) (Carpenter 1988, Dietrich & McKamey 1995). The option "nelsen" (ne) was used to construct a strict, consensus cladogram (Pape 1992, Marinoni & Carvalho 1993).

Characters and Character States Used in the Analysis

The characters used in the analysis are listed and discussed in the same sequence as they appear in the cladogram (Figs. 323–324). The letters A and P represent the relative apomorphic (derived) and plesiomorphic (primitive) conditions respectively.

1a. Larval feeding behavior: P (0) feeding on Diplopoda; A (1) feeding as a parasitoid or predator on terrestrial or aquatic Mollusca.

This is one of just a few characters in the matrix that establishes the monophyly of Salticellinae + Sciomyzinae. The genus *Pelidnoptera* is a parasitoid on Diplopoda, and numerous larval characters distinguish it from the larvae of Sciomyzidae (Vala et al. 1990). Although malacophagy characterizes nearly all Sciomyzidae and is a synapomorphy for the family, there is at least one species, *Sepedonella nana* Verbeke, that feeds on oligochaetes (Vala et al. 2000) as a secondary departure from the groundplan of the more basal clades of the family.

1b. Ventral arch in the larval cephalopharyngeal skeleton: P (0) absent; A (1) present.

The serrated ventral arch articulates with the ventral margin of the larval mouth hooks. This is the only larval structural character that is an autapomorphy for Salticellinae + Sciomyzinae and may be related with the malacophagous feeding behavior.

2. Number of spermathecae: P (0) three; A (1) two; A (2) four.

According to McAlpine (1989) the immediate ancestor of Muscomorpha had three sclerotized spermathecae. This is the basic number in the main sections of Muscomorpha: Aschiza, Schizophora, Acalyptatae, and Calyptratae. In *Pelidnoptera*, the

Table 1.—Matrix of taxa and character states.

	000 123	000 456	000 789	111 012	111 345	111 678	122 901	222 234	222 567	223 890	333 123	333 456	3 7
<i>Pelidnoptera</i>	001	010	001	000	000	000	000	000	000	000	000	000	0
<i>Salticella</i>	120	010	000	020	000	000	000	000	000	000	000	000	0
<i>Sciomyza</i>	110	120	110	101	000	000	000	000	000	000	000	000	0
<i>Oidematops</i>	110	020	110	101	000	000	000	000	000	000	000	000	0
<i>Atrichomelina</i>	110	120	110	100	000	000	000	000	000	000	000	000	0
<i>Tetanura</i>	110	102	110	110	000	000	000	000	010	000	100	000	0
<i>Colobaea</i>	111	110	110	110	000	000	000	000	000	000	000	000	0
<i>Calliscia</i>	110	110	110	000	100	010	000	000	000	000	000	000	0
<i>Parectinocera</i>	110	010	110	000	100	000	000	000	000	000	000	000	0
<i>Pteromicra</i>	110	010	110	000	000	000	000	000	000	000	000	000	0
<i>Pherbellia</i>	110	010	110	000	000	000	000	000	000	000	000	000	0
<i>Eutrichomelina</i>	111	101	001	000	001	000	000	000	000	000	000	000	0
<i>Ectinocera</i>	111	101	001	000	011	000	001	000	000	010	000	000	0
<i>Renocera</i>	111	101	001	000	011	000	000	000	000	000	000	000	0
<i>Antichaeta</i>	111	101	100	020	010	100	000	100	000	000	000	000	0
<i>Chasmacryptum</i>	111	101	001	000	011	110	000	000	000	000	000	000	0
<i>Shannonia</i>	111	101	001	000	000	112	001	000	000	000	000	000	0
<i>Perilimnia</i>	111	101	001	000	000	112	001	000	000	000	000	000	0
<i>Hoplodictya</i>	111	101	001	000	012	112	101	000	000	000	000	000	0
<i>Dictya</i>	111	101	001	000	012	112	100	000	000	000	000	000	0
<i>Hydromya</i>	111	101	001	000	011	112	110	000	000	000	000	000	0
<i>Neolimnia</i>	111	101	000	000	011	112	110	000	000	000	000	000	0
<i>Tetanoceroides</i>	111	101	011	010	011	112	110	000	000	000	000	000	0
<i>Euthycerina</i>	111	102	001	000	011	112	110	000	000	000	000	000	0
<i>Tetanocera</i>	111	102	001	000	011	112	110	000	000	000	000	000	0
<i>Trypetolimnia</i>	111	102	001	010	011	111	110	000	000	000	000	000	0
<i>Psacadina</i>	111	102	000	000	011	112	110	000	000	000	000	000	0
<i>Steyskalina</i>	111	102	000	000	011	112	110	000	000	000	000	000	0
<i>Dictyodes</i>	111	101	001	010	012	112	110	110	000	000	000	000	0
<i>Ilione</i>	111	101	001	010	011	112	110	100	000	000	000	000	0
<i>Pherbina</i>	111	101	001	010	011	112	110	100	000	000	000	000	0
<i>Trypetoptera</i>	111	101	001	010	011	112	110	100	000	000	000	000	0
<i>Limnia</i>	111	101	001	000	011	111	120	100	000	000	000	000	0
<i>Poecilographa</i>	111	101	001	010	011	112	130	100	000	000	000	000	0
<i>Pherbecta</i>	111	101	001	010	011	112	130	111	000	000	000	000	0
<i>Protodictya</i>	111	101	001	010	011	112	130	111	000	000	000	000	0
<i>Guatemalaia</i>	111	101	001	010	011	112	110	000	100	000	000	000	0
<i>Elgiva</i>	111	102	001	000	011	112	110	000	111	000	000	000	0
<i>Hedria</i>	111	101	001	010	011	111	110	000	110	001	000	000	0
<i>Dichetophora</i>	111	101	001	010	011	111	110	000	111	000	110	000	0
<i>Coremacera</i>	111	101	001	000	011	111	120	000	101	000	000	000	0
<i>Dictyacium</i>	111	101	001	000	011	101	120	000	101	000	000	000	0
<i>Euthycera</i>	111	101	001	000	011	111	120	000	101	000	000	000	0
<i>Ethiolimnia</i>	111	101	000	000	011	003	120	000	010	110	000	000	0
<i>Teutoniomya</i>	111	101	001	0?0	011	11?	220	000	210	010	000	100	0
<i>Thecomyia</i>	111	102	001	000	011	113	220	000	110	111	111	010	0
<i>Sepedoninus</i>	111	102	101	000	012	113	230	000	110	111	111	110	0
<i>Sepedonella</i>	111	102	102	020	012	113	200	000	111	111	111	111	0
<i>Sepedon</i>	111	102	101	020	012	113	230	000	210	111	110	111	0
<i>Sepedomerus</i>	111	102	101	020	012	113	230	000	210	111	110	111	1
<i>Sepedonea</i>	111	102	102	020	012	113	230	000	210	111	110	111	1

number of spermathecae is also three, this number being considered the plesiomorphic condition for the Sciomyzidae. Only in *Salticella* is the number of spermathecae four, which we interpret to be a secondary condition, probably being derived from two. Thus, four spermathecae are an autapomorphy for the Salticellinae, and two spermathecae remain a synapomorphy for Sciomyzinae.

3. Position of sixth left abdominal spiracle of the male (Figs. 115–159): P (0) in membrane; A (1) in sclerotized tergite.

Within the Sciomyzidae the abdominal spiracles of males may occur in the membrane or the sclerotized tergite. Primitively in Muscomorpha, the spiracles are in the membrane, which is considered the plesiomorphic condition for the Sciomyzidae. The position of the sixth spiracle in the sclerotized portion of the tergite is a synapomorphy for the Tetanocerini. Males of *Colobaea* Zetterstedt have the spiracle in the sclerotized tergite, a condition that probably represents a secondary reversal.

4. Sixth abdominal tergite of the male (Figs. 69, 74–76): P (0) present; A (1) absent.

Having all abdominal sclerites present is undoubtedly the plesiomorphic condition. According to McAlpine (1989) the reduction of the sixth abdominal tergite in males is an apomorphy for the superfamily Sciomyzoidea. Griffiths (1972) considered this reduction to be a synapomorphy, confirming the monophyly of Sciomyzidae. In Sciomyzidae, however, there is a complete absence of this tergite in most genera. Only in *Salticella* and in four genera of Sciomyzini, *Oidematops* Cresson, *Parectinocera* Becker, *Pherbellia*, and *Pteromicra* Lioy, is there a sixth tergite, which, however, is reduced.

5. Subepandrial plate (Figs. 161–169, 197): A (0) absent; P (1) vestigial; A (2) well developed.

The common, plesiomorphic condition, is the presence of a vestigial subepandrial plate found in *Pelidnoptera*, *Salticella*, *Co-*

lobaea, *Calliscia* Steyskal, *Parectinocera*, *Pteromicra*, and *Pherbellia*. It is lacking in all genera of the Tetanocerini. In *Sciomyza* Fallén, *Oidematops*, and *Atrichomelina* Cresson, the subepandrial plate is well developed and is a synapomorphic condition that characterizes these three genera. In *Tetanura* (tribe Sciomyzini), the plate is also absent, a condition we consider to be homoplastic.

6. Anterior surstylus (Figs. 161–203): P (0) well developed; A (1) vestigial; A (2) absent.

The transformation series for this character is linear: 0 → 1 → 2. *Pelidnoptera* has two pairs of well-developed, paired surstyli, and thus the presence of an anterior well-developed surstylus is the plesiomorphic condition for this character. Within the Sciomyzidae, the tribe Sciomyzini also has an anterior, well-developed surstylus. The genera *Tetanura* (tribe Sciomyzini) and *Elgiva* Meigen; the assemblage formed by the genera *Euthycerina* Malloch, *Tetanocera*, *Trypetolimnia* Mayer, *Psacadina* Enderlein, and *Steyskalina* Knutson; and the group of *Thecomyia* Perty, *Sepedoninus* Verbeke, *Sepedonella* Verbeke, *Sepedon*, *Sepedomerus* Steyskal + *Sepedonea* Steyskal; lack an anterior surstylus, having only the posterior one. The remaining genera of Tetanocerini have a vestigial, anterior surstylus.

7. Shape of aedeagus (Figs. 61–63, 66–67, 204–322): P (0) asymmetrical; A (1) symmetrical.

Asymmetry in the postabdomen of male Acalyptratae may involve internal structures, including the aedeagus. Within genera of Sciomyzidae, the aedeagus demonstrates great variation in shape and symmetry. *Pelidnoptera* has an asymmetrical aedeagus, a condition that is considered to be plesiomorphic. In most Tetanocerini, except for *Antichaeta*, the aedeagus is a complex structure with several completely asymmetrical sclerites. In the Sciomyzini and in the group of *Sepedoninus*, *Sepedo-*

nella, *Sepedon*, *Sepedomerus* + *Sepedonea*, the aedeagus is completely symmetrical.

8. Attachment of gonopod (Figs. 204–322): P (0) fused to the hypandrium; A (1) free.

McAlpine (1989) postulated the fusion of the gonopod to the hypandrium as a plesiomorphic condition for the Acalyptratae. All groups examined that are closely related to the Sciomyzidae have the gonopod fused to the hypandrium. The presence of a gonopod that is well developed and free is a condition that supports the monophyly of the tribe Sciomyzini. In *Tetanoceroides* Malloch, a free gonopod is apparently homoplastic.

9. Paramere (Figs. 204–322): A (0) not digitiform, elongate and well developed; P (1) digitiform and well developed; A (2) absent.

Pelidnoptera has a digitiform, well-developed paramere that is considered to be plesiomorphic. In *Salticella*, the paramere is elongate and well developed, as in the Sciomyzini and in the genera *Antichaeta*, *Pscadina*, *Neolimnia*, *Ethiolimnia*, and *Steyskalina*. Two genera, *Sepedonea* and *Sepedonella*, lack a paramere, a condition that is considered homoplastic.

10. Shape of aedeagal apex (Figs. 204–213): P (0) variously shaped, but not flattened; A (1) flattened.

The presence of an aedeagus with a flattened apex is a synapomorphy for the group of *Sciomyza*, *Oidematops*, *Atrichomelina*, *Tetanura*, and *Colobaea* within the Sciomyzini.

11. Basiphallus (Figs. 203–322): P (0) well developed; A (1) present but poorly developed; A (2) absent.

This character has the greatest number of steps in the matrix and analysis, indicating a large number of homoplasies and reversals. The taxa that have the intermediate apomorphic condition, the basiphallus poorly developed, are *Colobaea*, *Tetanura*, *Trypetolimnia*, *Tetanoceroides*, *Dictyodes* Malloch, *Ilione* Verbeke, *Pherbina* Robineau-Desvoidy, *Trypetoptera* Hendel, *Gua-*

temalia Steyskal, *Hedria* Steyskal, *Diche-tophora* Rondani, *Poecilographa* Melander, *Protodictya* Malloch + *Pherbecta* Steyskal (the later two genera are sister groups, as indicated by the “+” connection). The genera *Salticella*, *Antichaeta*, *Sepedonella*, *Sepedon*, *Sepedomerus*, and *Sepedonea* lack a basiphallus. The remaining genera have a well-developed basiphallus.

12. Setal investment of foretibia: P (0) without preapical setae; A (1) bearing a pair of preapical setae.

The presence of a pair of preapical setae on the foretibia is a synapomorphy for *Oidematops* and *Sciomyza*.

13. Vestiture of the aedeagus (Figs. 214–217): P (0) without scalelike structures; A (1) with scalelike structures.

In *Calliscia* and *Parectinocera*, the aedeagus is covered with small scalelike structures, a synapomorphy for these genera.

14. Proepisternal seta: P (0) present; A (1) absent.

Steyskal (1965) used the presence of the proepisternal seta to distinguish the tribe Sciomyzini from the Tetanocerini. Most genera of Tetanocerini lack this seta, although *Shannonia* Malloch and *Perilimnia* Becker possess one. For the latter genera this condition is considered to be homoplastic.

15. Male terminalia (Figs. 57–59, 64–65, 68–160): P (0) with the 6th, 7th, and 8th sternites separated, the 6th and 7th asymmetrical; A (1) with the synsternite 7+8 and 6th sternite separated and asymmetrical; A (2) with the synsternite 6+7+8 symmetrical.

According to Steyskal (1957) the asymmetry of the male Acalyptratae postabdomen, including segments beyond the fifth, is due to three basic movements within the pupa: circumversion, reflection, and “strophe.” The symmetry may occur as a result of the obliteration of these movements. Asymmetry in Sciomyzidae is restricted to the sixth, seventh, and eighth segments. There is a modification gradient of these

segments, changing from completely asymmetrical to completely symmetrical, associated to the fusion of the segments mentioned above.

16. Placement of sixth right abdominal spiracle of the male (Figs. 68–114): P (0) in membrane; A (1) in sclerotized tergite.

Sciomyzini and *Eutrichomelina*, *Rencera* Hendel, and *Ectinocera* Zetterstedt have the plesiomorphic condition of this character, the spiracle is in the membrane. From *Antichaeta* to *Sepedonea*, the spiracle is in the tergite. In *Ethiolimnia*, there is a reversal to the plesiomorphic condition.

17. Placement of seventh right abdominal spiracle of the male (Figs. 68–114): P (0) in membrane; A (1) in sclerotized tergite.

The plesiomorphic condition occurs in most Sciomyzini except for *Calliscia*. From *Chasmacryptum* Becker to *Sepedonea* most genera have the spiracle in the tergite, except for *Dictyacium* Steyskal and *Ethiolimnia*.

18. Shape of head: P (0) as in Fig. 52a; A (1) as in Fig. 52b; A (2) as in Fig. 52c; A (3) as in Fig. 52d.

The head, from the ancestor to *Chasmacryptum*, has the shape shown in Fig. 52a. Beyond the group of *Shannonia* + *Perilimnia* the intermediate apomorphic condition, represented by Fig. 52c, is present. From this state the other two apomorphic states evolved. The pattern of head shape, as in Fig. 52b, is present in *Trypetolimnia* and *Limnia* Robineau-Desvoidy as homoplasies and in *Hedria*, *Dichetophora*, *Coremacera* Rondani, *Dictyacium*, and *Euthycera* Latreille. The shape, as in Fig. 52d, defines the group of *Ethiolimnia*, *Thecomyia*, *Sepedoninus*, *Sepedonella*, *Sepedon*, *Sepedomeris*, and *Sepedonea*. Because *Teutoniomyia* Hennig has a very different head, compared to other genera, this character was coded as missing in the matrix (Table 1).

19. Proportion between the length of the pedicel and first flagellomere (Figs. 1–51): P (0) pedicel approximately half of first flagellomere; A (1) pedicel subequal to the

length of the first flagellomere; A (2) pedicel approximately twice the length of the first flagellomere.

The plesiomorphic condition is present from Sciomyzini until *Shannonia* + *Perilimnia*. From this group to *Ethiolimnia* the intermediate apomorphic condition (1) is present. The apomorphic condition (2) is present in the following genera: *Teutoniomyia*, *Thecomyia*, *Sepedoninus*, *Sepedonella*, *Sepedon*, *Sepedomeris*, and *Sepedonea*.

20. Condition of sternites of female terminalia (Figs. 53–56): P (0) with sternites 6th, 7th, and 8th separate; A (1) with 6th separate and 7th and 8th fused; A (2) 6th, 7th, and 8th incompletely fused; A (3) 6th, 7th, and 8th completely fused.

The transformation series was linear. Two lineages arose from state 1. One of these goes through the third state and the second goes through the fourth state. The evolution occurred from separated sternites passing through steps of fusion to the complete fusion of 6th, 7th, and 8th. All Sciomyzini and the Tetanocerine genera until *Hoplodictya* Cresson + *Dictya* Meigen have sternites 6th, 7th, and 8th separate. From the polytomy of *Hydromya* Robineau-Desvoidy to the ancestor of *Ethiolimnia* the 7th and 8th sternites are fused. *Protodictya* + *Pherbecta* and *Poecilographa* have the three sternites completely fused as *Sepedoninus*, *Sepedon*, *Sepedomeris*, and *Sepedonea*. In *Sepedonella*, a genus belonging to this group, the three sternites are separate. The monophyletic group formed by *Coremacera*, *Dictyacium*, and *Euthycera*, and the genera *Limnia*, *Teutoniomyia*, and *Thecomyia* have the sternites 6, 7, and 8 almost fused. Lines separating these sternites are perceptible.

21. Aedeagus with lobed apex (Figs. 222–224, 230–238): P (0) absent; A (1) present.

Ectinocera, *Hoplodictya*, and *Perilimnia* + *Shannonia* have the aedeagus with the distal end lobed. This character apparently appeared independently in these genera. In

the other genera, the distal end of the aedeagus has several different shapes.

22. Subalar setae: P (0) absent; A (1) present.

The subalar setae are present in *Dictyodes*, *Ilione*, *Pherbina*, *Trypetoptera*, *Limnia*, *Poecilographa*, *Pherbecta* + *Protodictya*. The apomorphic state apparently evolved independently in *Antichaeta*.

23. Aedeagus convoluted as in Figs. 263–265, 281–286: P (0) absent; A (1) present.

A convoluted aedeagus occurs in *Protodictya*, *Pherbecta*, and *Dictyodes*. For *Protodictya* and *Pherbecta* this character defines the common ancestor.

24. Fourth abdominal sternite of the male fused to fifth, forming a medioapical process: P (0) absent; A (1) present.

The presence of a well-developed, medioapical process in the fifth abdominal sternite of the male as a complex structure is a synapomorphy for the species of *Protodictya* (Marinoni & Knutson 1992, Marinoni & Carvalho 1993). In *Pherbecta*, however, there is, at the same position, a process that is less well developed and which may be homologous to that of *Protodictya*.

25. Lunula: P (0) not exposed; A (1) exposed; A (2) greatly exposed.

In the outgroup, *Pelidnoptera*, genera of Sciomyzini, and genera of Tetanocerini from *Eutrichomelina* to *Protodictya*, the lunula is not exposed. From *Guatemala* to *Sepedonella*, the intermediate state (1) is present. In *Ethiolimnia*, there is a reversal to the plesiomorphic state. In the apical genera, *Sepedon*, *Sepedomerus*, and *Sepedonea*, the lunula is greatly exposed, which is interpreted as an even more derived condition from the intermediate state. In *Teutoniomyia*, which also has a greatly exposed lunula, this character state is homoplastic.

26. Presutural supra-alar setae: P (0) present; A (1) absent.

The plesiomorphic condition of this character is the presence of presutural supra-alar setae. The absence of these setae is a syn-

apomorphy for the group *Elgiva*, *Hedria*, *Dichetophora*, *Ethiolimnia*, *Teutoniomyia*, *Thecomyia*, *Sepedoninus*, *Sepedonella*, *Sepedon*, *Sepedomerus*, and *Sepedonea*. In *Coremacera*, *Dictyacium*, and *Euthycera*, there is a reversal to the plesiomorphic state. *Tetanura* has this seta, a condition that is considered homoplastic.

27. Seventh and 8th abdominal tergites of the female: P (0) separate; A (1) fused.

The fusion of the 7th and the 8th abdominal tergites of the female is a character state that links the genera *Dichetophora*, *Coremacera*, *Dictyacium*, and *Euthycera*. In *Elgiva* and *Sepedonella*, the fusion is homoplastic.

28. Prominent eyes: (0) absent; (1) present.

Ethiolimnia, *Thecomyia*, *Sepedoninus*, *Sepedonella*, *Sepedon*, *Sepedomerus*, and *Sepedonea* have prominent eyes, a synapomorphy for these genera. As *Ethiolimnia* is in a polytomy with *Teutoniomyia*, prominent eyes are a confirmed synapomorphy for *Thecomyia*, *Sepedoninus*, *Sepedonella*, *Sepedon*, *Sepedomerus*, and *Sepedonea* and only perhaps for *Ethiolimnia*.

29. Number of postalar setae: P (0) 2; A (1) 0–1.

The presence of two postalar setae is the plesiomorphic condition. In *Ectinocera* and in the genera beyond *Ethiolimnia*, the number of postalar setae is reduced to one or none.

30. Ocellar setae: P (0) present; A (1) absent.

The presence of a pair of strong ocellar setae has been considered a plesiomorphic condition for the Muscomorpha (McAlpine 1989). In *Pelidnoptera*, these setae are present, as they are in most Sciomyzidae, including *Salticella*. These setae are absent in *Hedria* and in the group of *Thecomyia*, *Sepedoninus*, *Sepedonella*, *Sepedomerus* + *Sepedonea*.

31. Postpronotal setae: P (0) present; A (1) absent.

Most Sciomyzidae have postpronotal setae. The absence of these setae character-

izes the group of genera beyond *Thecomyia*. In *Dichetophora* and *Tetanura*, the absence of postpronotal setae is considered to be homoplastic.

32. Number of scutellar setae: P (0) 2 pairs; A (1) 1 pair.

Primitively the family Sciomyzidae has two pairs of scutellar setae. One pair of scutellar setae occurs in *Dichetophora* and the group of genera beyond *Thecomyia*.

33. Number of notopleural setae: P (0) 2; A (1) 1.

Two notopleural setae are present in most Sciomyzidae and in *Pelidnoptera*. Only the genera *Thecomyia*, *Sepedoninus*, and *Sepedonella* have a single notopleural seta. A reversal of this characters to the plesiomorphic state of two notopleural setae occurs in the genera *Sepedon*, *Sepedomerus*, and *Sepedonea*.

34. Hindtibia arch-shaped: P (0) absent; A (1) present.

The genera *Teutoniomyia*, *Sepedoninus*, *Sepedonella*, *Sepedon*, *Sepedomerus*, and *Sepedonea* have an arch-shaped hindtibia. Only *Thecomyia* does not have the hindtibia arch-shaped.

35. Head with sutures: P (0) distinct; A (1) indistinct.

The head sutures of *Thecomyia*, *Sepedoninus*, *Sepedonella*, *Sepedon*, *Sepedomerus*, and *Sepedonea* are indistinct. This condition is considered a synapomorphy for this group.

36. Epandrium (Figs. 68–160): P (0) free; A (1) fused to the 8th sternite.

The fusion of the epandrium to the 8th sternite is a synapomorphy for the genera *Sepedonella*, *Sepedon*, *Sepedomerus*, and *Sepedonea*.

37. Hindtibia with a spinelike projection: P (0) absent; A (1) present.

In most Sciomyzidae, there is no projection from the hindtibia. *Sepedonea* and *Sepedomerus* have a hindtibia that bears a spinelike projection, which is a synapomorphy that links these two genera.

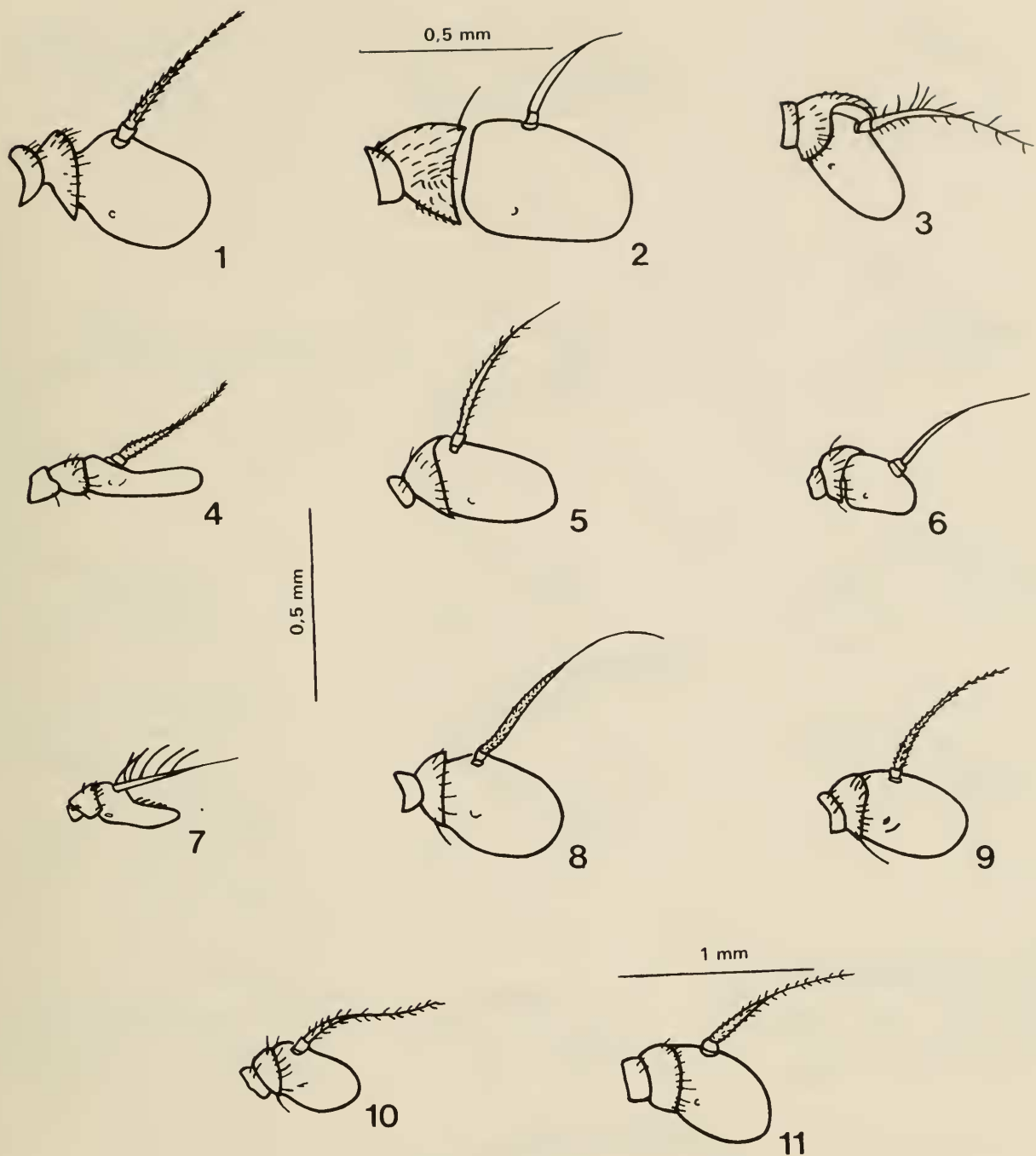
Discussion

Relationships.—The monophyly of the Sciomyzidae is defined by a behavioral character, the larvae are predators or parasitoids on aquatic or terrestrial Mollusca (Berg 1953, Knutson et al. 1970, Griffiths 1972, Barnes 1979) and the presence of a serrate ventral arch below the mouth hooks in the larvae (Griffiths 1972). The serrate ventral arch could be closely correlated with the malacophagous feeding behavior.

The genus *Salticella*, representing the Salticellinae, remains at the base of the cladogram, being distinguished from the subfamily Sciomyzinae and its monophyly confirmed by the following three autapomorphies: four spermathecae; cell M narrowed apically (this character was not used in the analysis because of its variability among genera of Sciomyzidae); and three pairs of surstyli. Knutson et al. (1970), working on the biosystematics of *Salticella fasciata* (Meigen), concluded that this genus is more closely related to Sciomyzini than to the Tetanocerini in morphological and biological aspects. This relationship is corroborated in the present analysis.

Among genera of the subfamily Sciomyzinae, two main monophyletic clades were formed, the first including *Pherbellia*, *Pteromicra*, *Calliscia*, *Parectinocera*, *Tetanura*, *Colobaea*, *Atrichomelina*, *Oidematops*, and *Sciomyza*; and the second including the 40 remaining genera. The two clades are concordant with the tribes Sciomyzini and Tetanocerini of Steyskal (1965). The genus *Eutrichomelina*, which traditionally has been placed in the Sciomyzini, is shown to be allied to the Tetanocerini in this analysis.

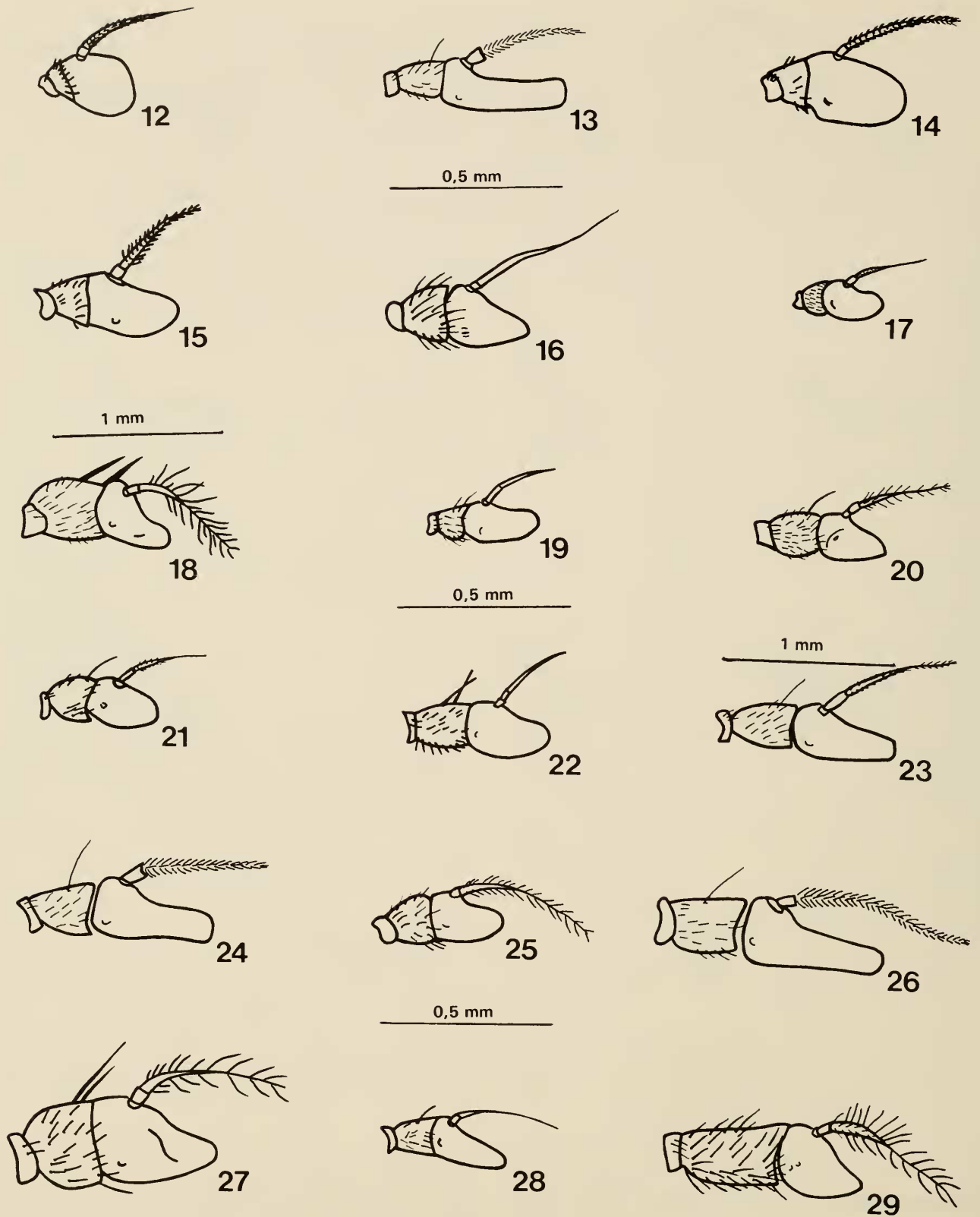
Behavioral aspects of the larvae have been discussed as possible synapomorphies for the tribes (Knutson & Lyneborg 1965, Abercrombie 1970). Toward one end of the scale, where the Sciomyzini are placed, the species that have been reared are parasitoids on stranded aquatic or terrestrial mollusks (*Colobaea* (Knutson



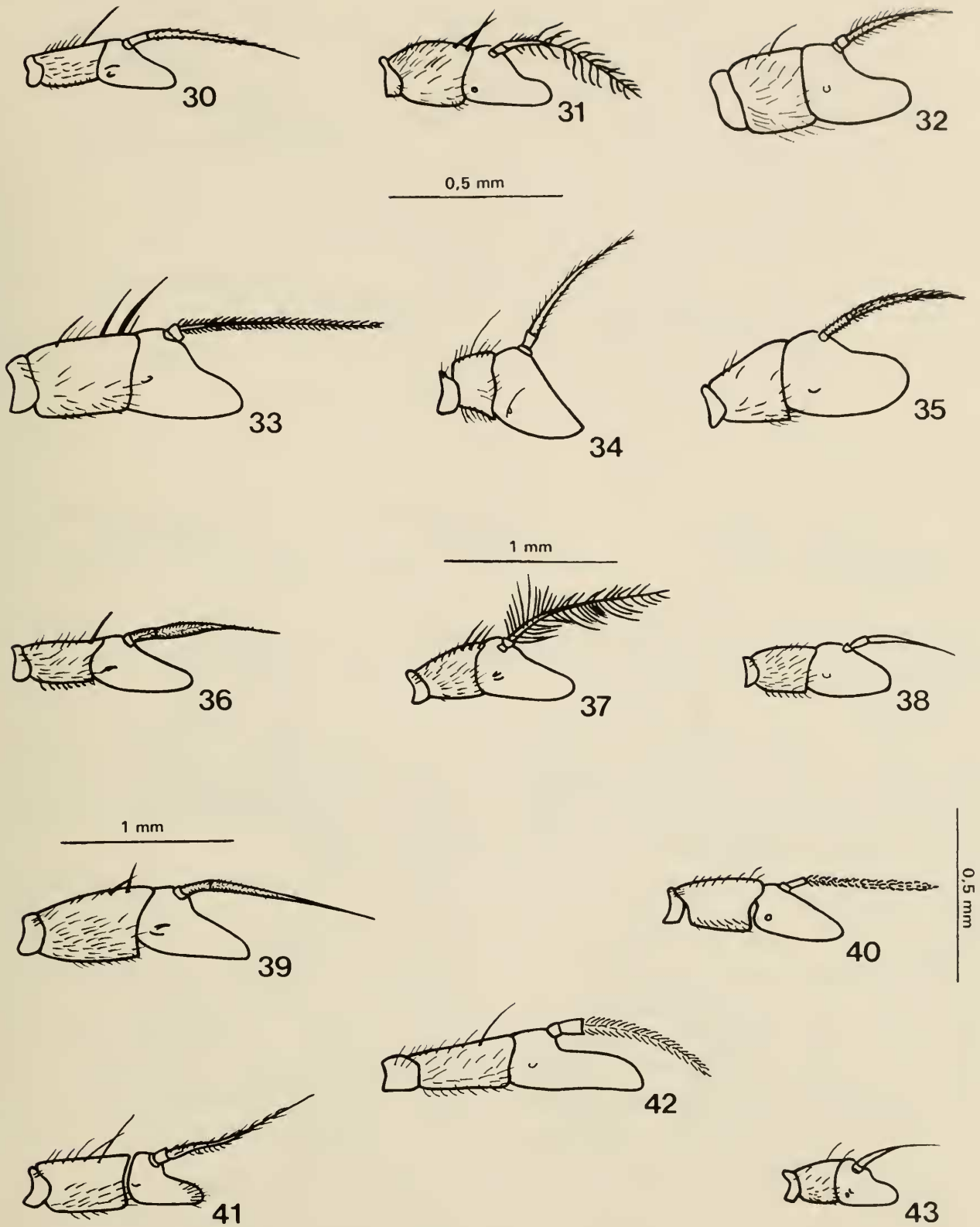
Figs. 1–11. Right antenna, right lateral view: 1, *Pelidnoptera*; 2, *Salticella*; 3, *Sciomyza*; 4, *Oidematops*; 5, *Atrichomelina*; 6, *Tetanura*; 7, *Colobaea*; 8, *Calliscia*; 9, *Parectinocera*; 10, *Pteromicra*; 11, *Pherbellia*. Fig. 11, scale = 1.0 mm; remaining Figs. scale = 0.5 mm.

1973); *Pherbellia* (Bratt et al. 1969); *Pteromicra* (Rozkošný & Knutson 1970); *Sciomyza* (Foote 1959); *Tetanura* (Knutson 1970)). Toward the other end, most Tetanocerini are predaceous on aquatic or terrestrial mollusks (*Coremacera* (Knutson 1973); *Dichetophora* (Vala et al. 1987); *Dictya* (Valley & Berg 1977); *Dictyodes* (Abercrombie 1970, Abercrombie & Berg 1978); *Elgiva* (Knutson & Berg 1964a, Orth & Knutson 1987); *Euthycera* (Vala et

al. 1983, Vala & Caillet 1985); *Hoplodictya* (Neff & Berg 1962); *Hydromya* (Knutson & Berg 1963); *Ilione* (Knutson & Berg 1964b); *Limnia* (Vala & Knutson 1990); *Perilimnia* (Kaczynski et al. 1969); *Pherbecta* (Knutson 1972); *Pherbina* (Knutson et al. 1975, Vala & Gasc 1990); *Protodictya* (Abercrombie 1970, Neff & Berg 1961); *Psacadina* (Knutson et al. 1975); *Renocera* (Foote & Knutson 1970); *Sepe-don* (Neff & Berg 1966, Knutson et al.



Figs. 12-29. Right antenna, right lateral view: 12, *Eutrichomelina*; 13, *Ectinocera*; 14, *Renocera*; 15, *Antichaeta*; 16, *Chasmacryptum*; 17, *Shannonia*; 18, *Perilimnia*; 19, *Hoplodictya*; 20, *Dictya*; 21, *Hydromya*; 22, *Neolimnia*; 23, *Tetanoceroides*; 24, *Euthycerina*; 25, *Tetanocera*; 26, *Trypetolimnia*; 27, *Psacadina*; 28, *Steyskalina*; 29, *Dictyodes*. Figs. 18 and 23 with scale 1.0 mm; the remaining Figs. 0.5 mm.

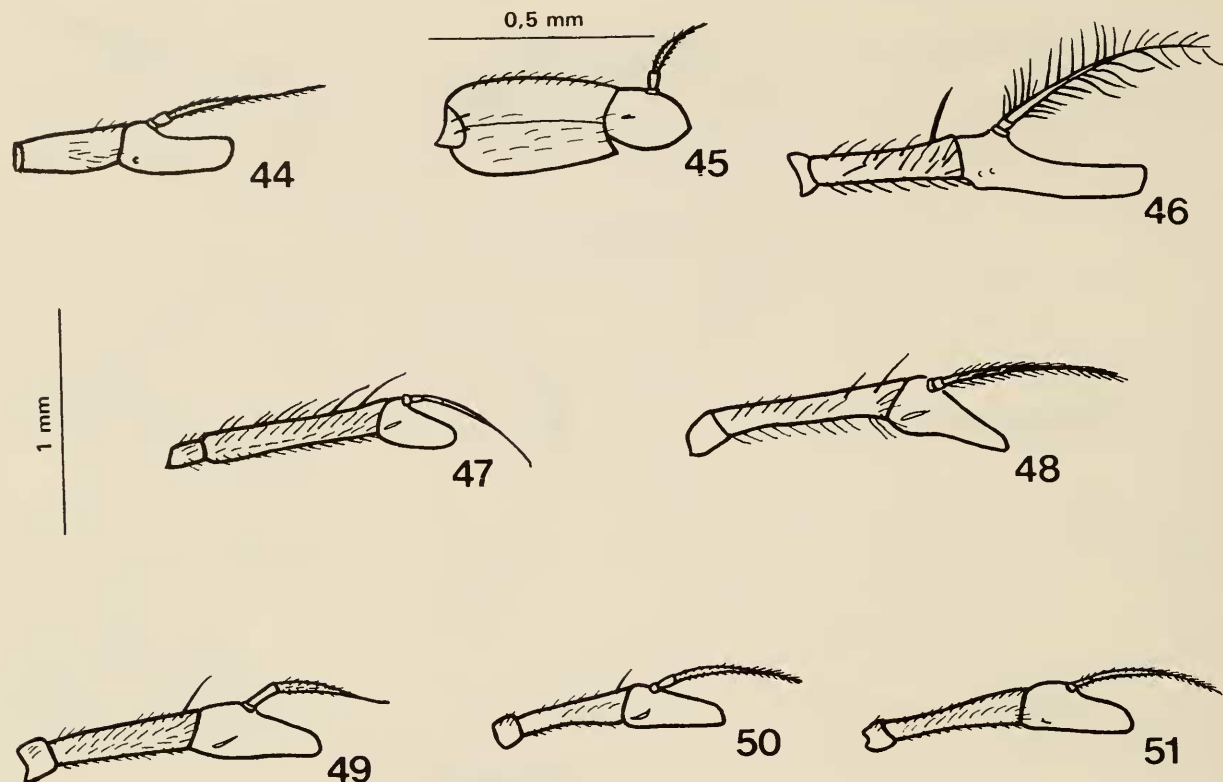


Figs. 30–43. Right antenna, right lateral view: 30, *Ilione*; 31, *Pherbina*; 32, *Trypetoptera*; 33, *Limnia*; 34, *Poecilographa*; 35, *Pherbecta*; 36, *Protodictya*; 37, *Guatemalaia*; 38, *Elgiva*; 39, *Hedria*; 40, *Dichetophora*; 41, *Coremacera*; 42, *Dictyaciun*; 43, *Euthycera*. Figs. 30–35 and 40 with scale 0.5 mm; Figs. 37–39 and 41–43 with scale 1.0 mm.

1967); *Sepedonea* (Abercrombie 1970, Knutson & Valley 1978); *Shannonia* (Kaczynski et al. 1969); *Tetanocera* (Knutson et al. 1965); *Tetanoceroides* (Abercrombie

1970); *Thecomyia* (Abercrombie & Berg 1975); *Trypetoptera* (Vala 1986)).

A few species of Sciomyzini and Tetanocerini, however, have an intermediate be-



Figs. 44–51. Right antenna, right lateral view: 44, *Ethiolimnia*; 45, *Teutoniomyia*; 46, *Thecomyia*; 47, *Sepedoninus*; 48, *Sepedonella*; 49, *Sepedon*; 50, *Sepedomerus*; 51, *Sepedonea*. Fig. 45 with scale 0.5 mm; the remaining Figs. with scale 1.0 mm.

havior between these two behaviors, i.e., sometimes they have parasitoid trends, sometimes predaceous. Examples of these kinds of behavior are evident in the species *Atrichomelina pubera* Loew and *Antichaeta analis* Zetterstedt. *Atrichomelina pubera* belongs to the Sciomyzini. Depending on circumstances this species has a predatory, parasitoid or even saprophagous behavior (Berg et al. 1959, Foote et al. 1960). Saprophagy may be the primitive condition, similar to that found in *Salticella* (Knutson et al. 1970) and the ancestor of Sciomyzidae (Abercrombie 1970). *Antichaeta analis* has some parasitoid characteristics, such as host specificity and oviposition on the host, but its behavior is predatory with the larvae feeding on snail eggs (Fisher & Orth 1964, Knutson 1966, Knutson & Abercrombie 1977).

More studies related to the evolution of the larval behavior are necessary to confirm that the larval habit is responsible for relationships among the genera within the family.

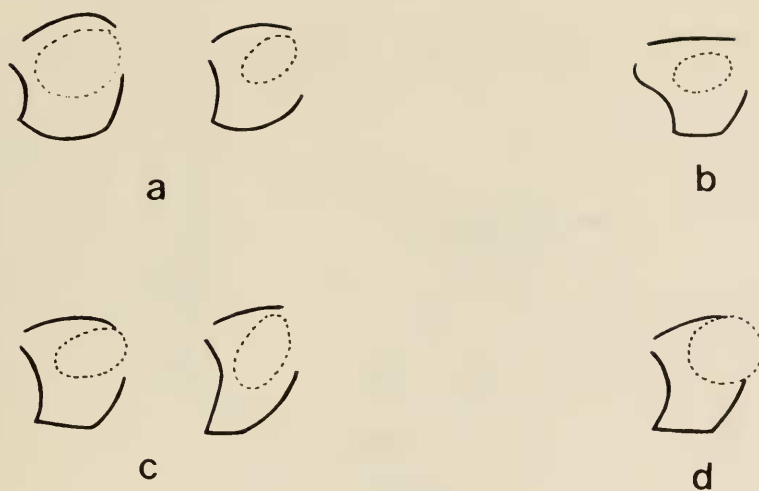
Most genera in the analysis remained in unresolved polytomies due to the great number of homoplasies and low number of synapomorphies.

Within the Sciomyzini, the relationships of *Pteromicra* and *Pherbellia* are not well resolved. Rozkošný & Knutson (1970), studying the biology and immature stages of *Pteromicra*, discovered that this genus is closely related to *Pherbellia*. However, even in our analysis, where these two genera are in close proximity on the cladogram, there is no adult character to corroborate this relationship.

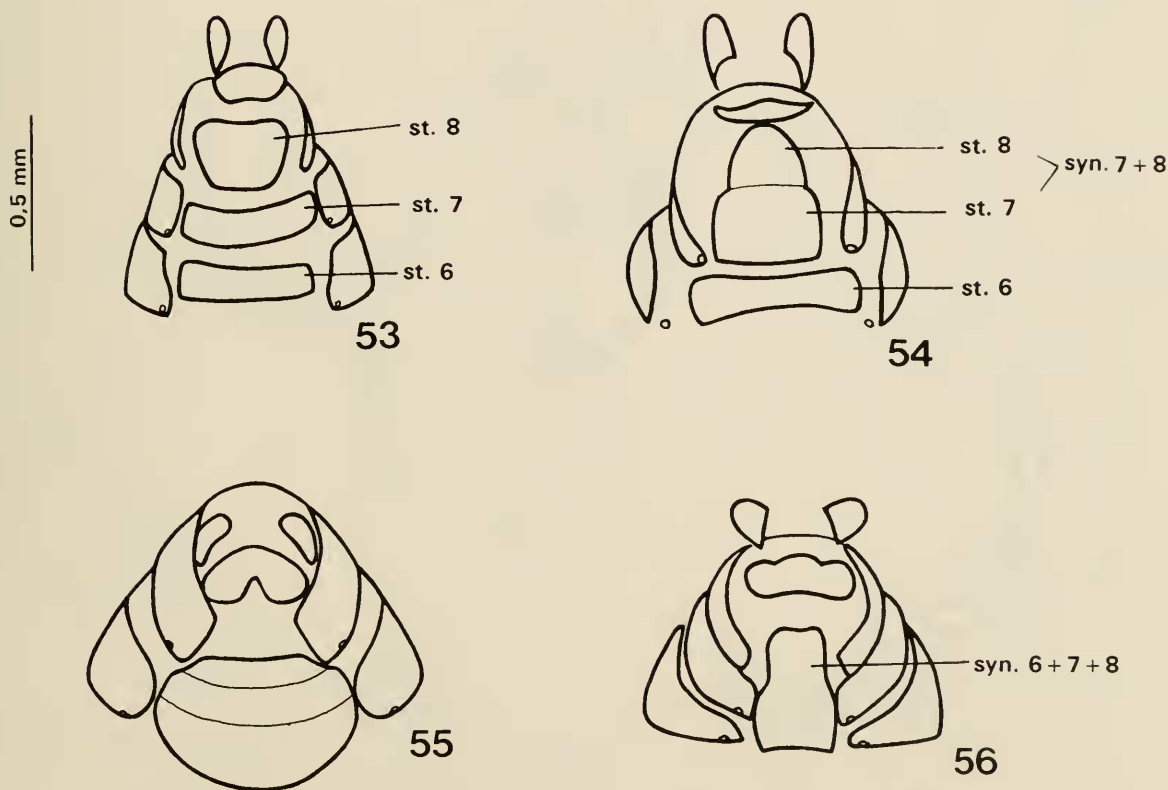
Knutson et al. (1990) considered *Colobaea*, *Pherbellia*, and *Pteromicra* to be related but did not elaborate any synapomorphies to support their grouping. In the same paper they also suggest that *Pherbellia* is paraphyletic.

Paractinocera and *Calliscia* appear in the analysis as having the same ancestor. These two genera are the only two within the Sciomyzini with Neotropical distributions.

The genera *Tetanura*, *Colobaea*, *Atricho-*



52

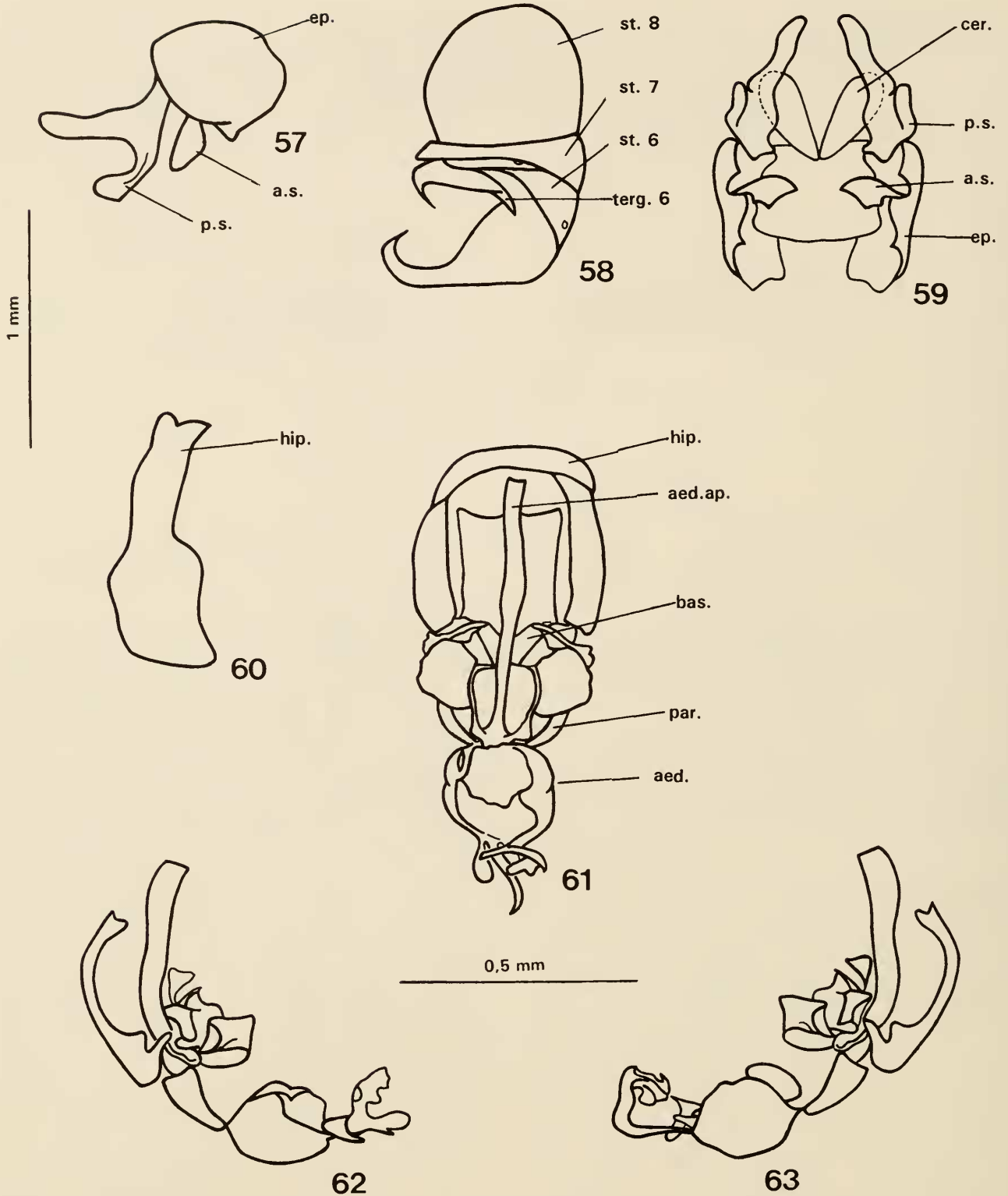


Figs. 52–56. 52. Shape of head: (a), State 0; (b), state 1; (c) state 2; (d) state 3. 53–56. Female terminalia, ventral view: 53, *Perilimnia*; 54, *Elgiva*; 55, *Coremacera*; 56, *Protodictya*. Sternite 6 (st. 6); sternite 7 (st. 7); sternite 8 (st. 8); synsternite 6+7+8 (syn. 6+7+8).

melina, *Sciomyza*, and *Oidematops* form a clade established by characters 4 and 10 (Figs. 323–324). In this group *Atrichomelina*, *Sciomyza* + *Oidematops* have their relationships well defined. The synapomorphic character that links the three genera is the

presence of a well-developed male subepandrial plate (Character 5). The other two genera remain in polytomy.

In the Tetanocerini, *Eutrichomelina*, *Ectinocera*, *Renocera*, *Antichaeta*, and *Chasmacroptum* are at the base of the clade. *Ec-*

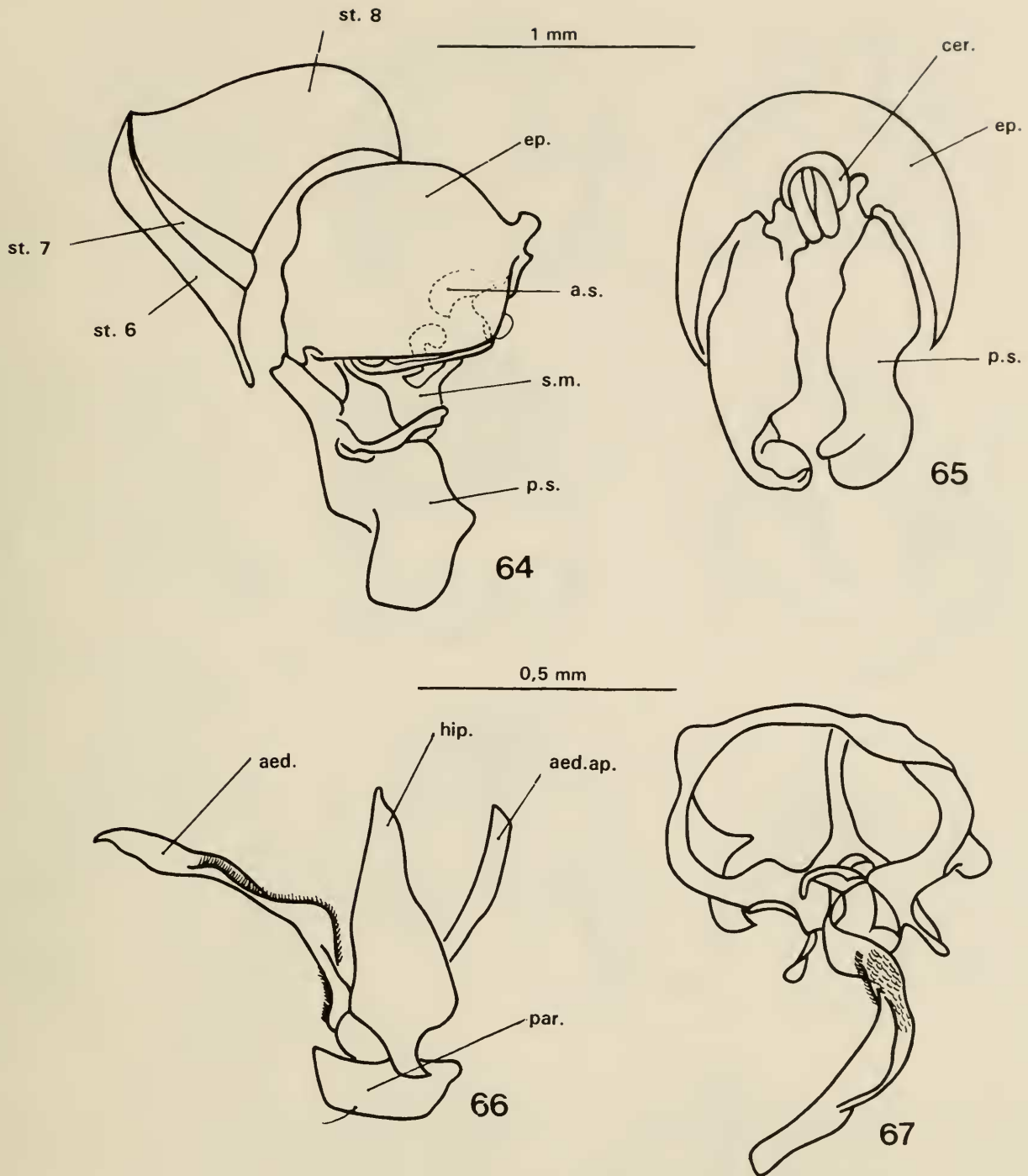


Figs. 57-63. Male terminalia. *Pelidnoptera*. Aedeagal apodeme (aed. ap.); basiphallus (bas.); cerci (cer.); aedeagal complex (aed. c.); epandrium (ep.); sternite 6 (st. 6); sternite 7 (st. 7); sternite 8 (st. 8); hypandrium (hip.); paramere (par.); subepandrial plate (sub. pl.); anterior surstylus (a. s.); posterior surstylus (p. s.). Figs. 57-60 with scale 1.0 mm; Figs. 61-63 with scale 0.5 mm.

tinocera and *Renocera* remain in polytomy. Steyskal (1959), using intuitive analysis, considered *Renocera*, *Chasmacryptum*, and *Tetanocera* to be morphologically related.

The uncertain position of *Antichaeta* was

already discussed by Fisher & Orth (1964) & Knutson (1966). Adult characters suggest that this genus belongs to the Tetanocerini, while larval characters indicate its position to be within the Sciomyzini. Boyes et al.

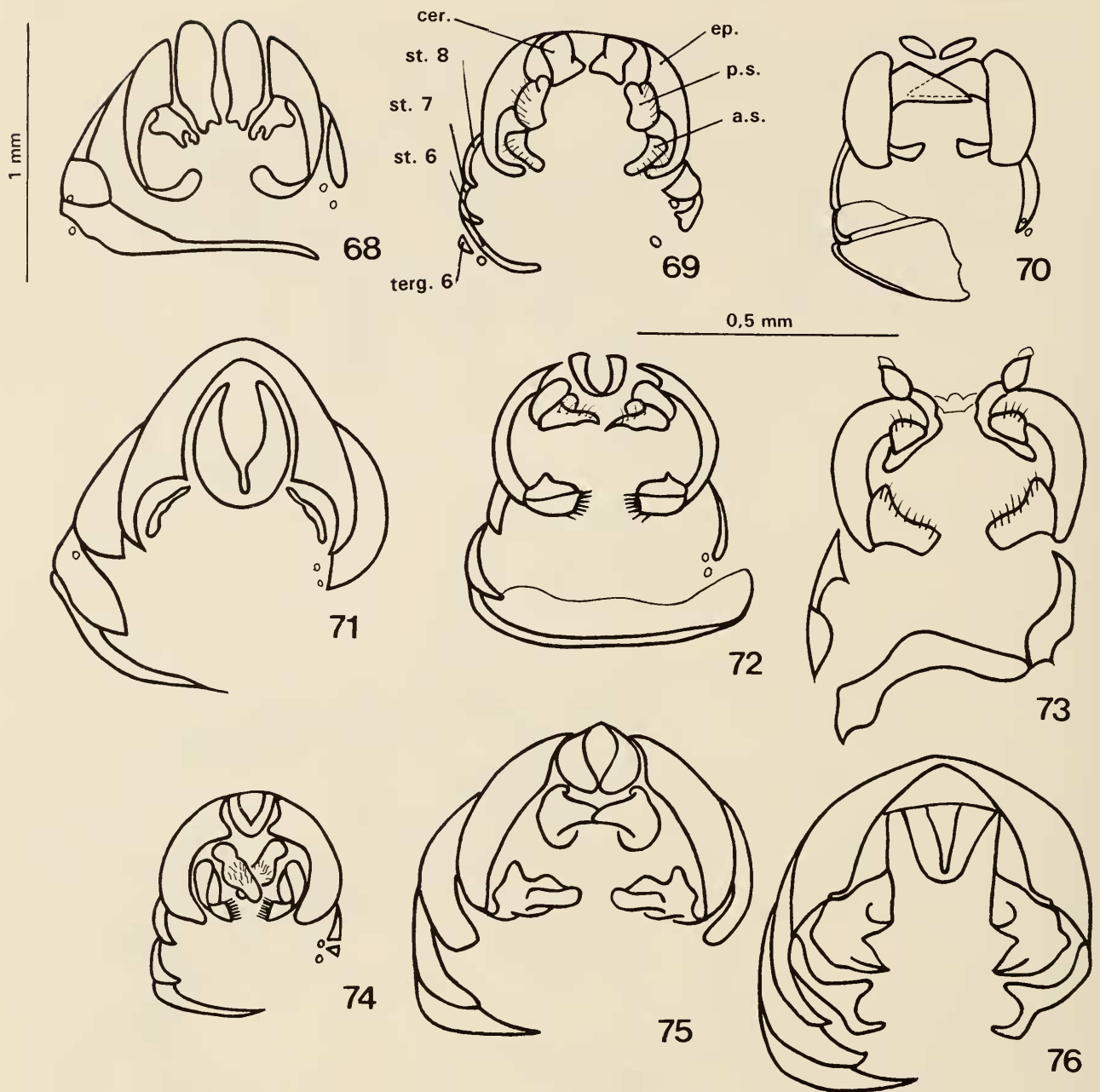


Figs. 64–67. Male terminalia. *Salticella*. Aedeagal apodeme (aed. ap.); cerci (cer.); aedeagal complex (aed. c.); epandrium (ep.); sternite 6 (st. 6); sternite 7 (st. 7); sternite 8 (st. 8); hypandrium (hip.); paramere (par.); anterior surstylus (a. s.); medial surstylus (s. m.); posterior surstylus (p. s.). Figs. 64–65 with scale 1.0 mm; Figs. 66–67 with scale 0.5 mm.

(1969), studying the karyotype of *Antichaeta melanosoma* Melander, observed its similarity with those of the Tetanocerini genera. In the present analysis, *Antichaeta* is placed in the Tetanocerini group of genera near *Chasmacryptum*.

After *Chasmacryptum*, the clade of *Shannonia* + *Perilimnia* appears as the sister group of the other genera. Kaczynski et al.

(1969) studied the biosystematics of the immature stages of these two genera and observed morphological and behavioral affinities between them. As observed by these authors, the main similarities between the larvae of *Shannonia* and *Perilimnia* are in the cephalopharyngeal skeleton. They also suggested the position of both genera within the Tetanocerini.

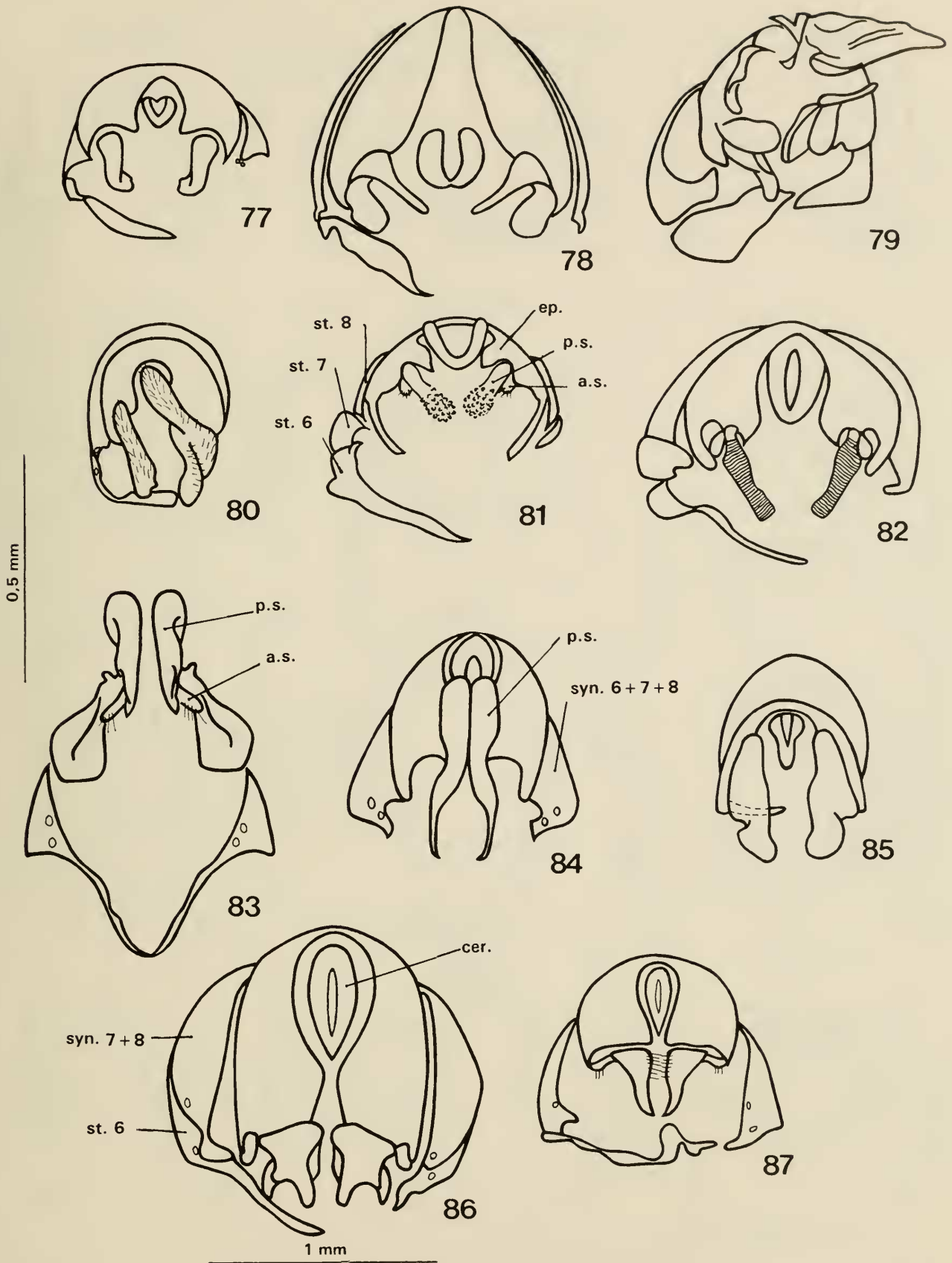


Figs. 68–76. Male terminalia, ventral view: 68, *Sciomyza*; 69, *Oidematops*; 70, *Atrichomelina*; 71, *Tetanura*; 72, *Colobaea*; 73, *Calliscia*; 74, *Parectinocera*; 75, *Pteromicra*; 76, *Pherbellia*. Cerci (cer.); epandrium (ep.); sternite 6 (st. 6); sternite 7 (st. 7); sternite 8 (st. 8); anterior surstylus (a. s.); posterior surstylus (p. s.); tergite 6 (terg. 6). Fig. 68 with scale 1.0 mm; the remaining Figs. with scale 0.5 mm.

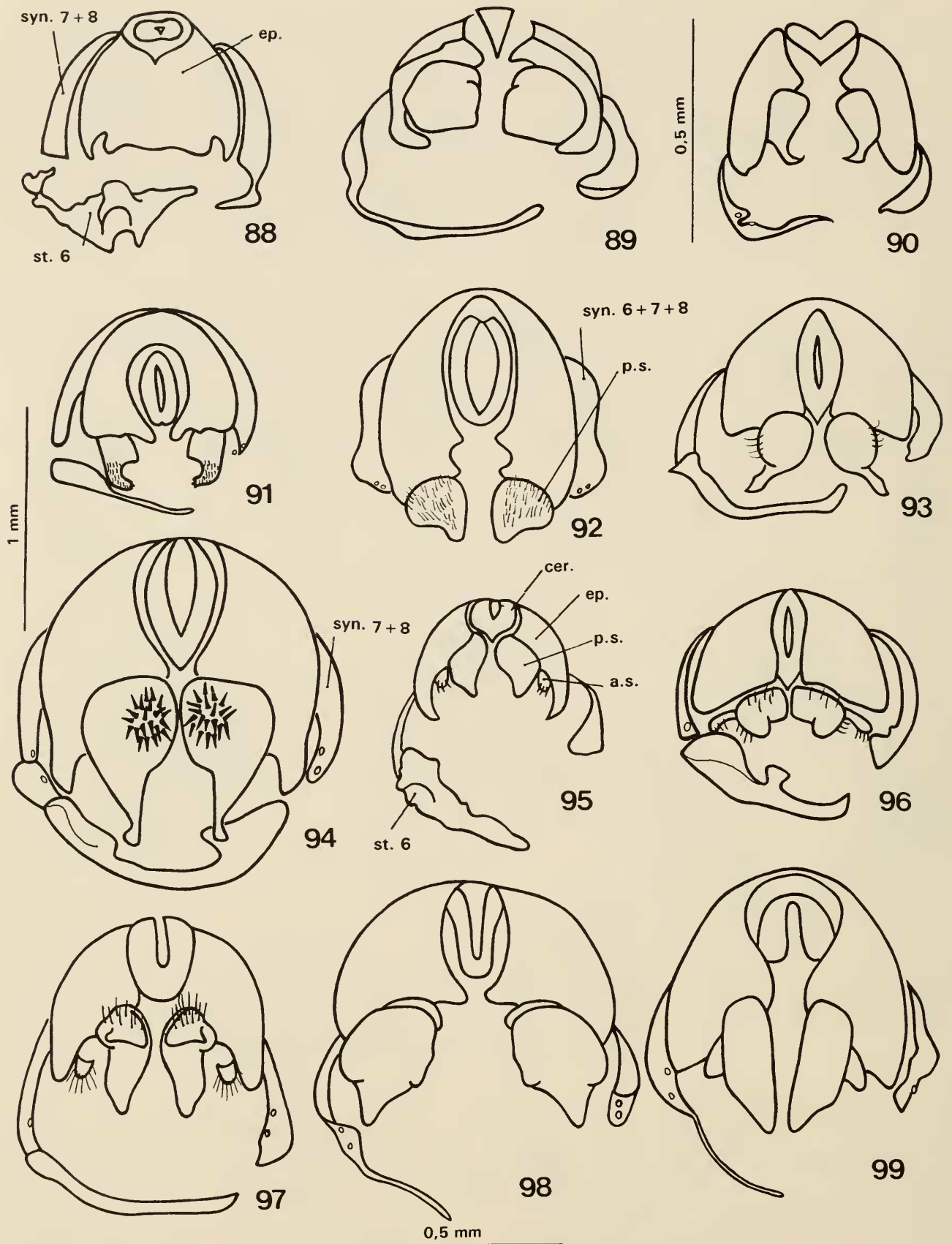
Hoplodictya + *Dictya* form the next clade. Boyes et al. (1969) compared its karyotypes and recognized the proximity of these two genera.

Hydromya, *Neolimnia*, and *Tetanoceroides* remain as a polytomy with three other groups formed. The components of one of these groups are: *Euthycerina*, *Tetanocera*, *Trypetolimnia*, *Psacadina*, and *Steyskalina*. The other group is formed by *Dictyodes*, *Ilione*, *Pherbina*, *Trypetoptera*, *Limnia*,

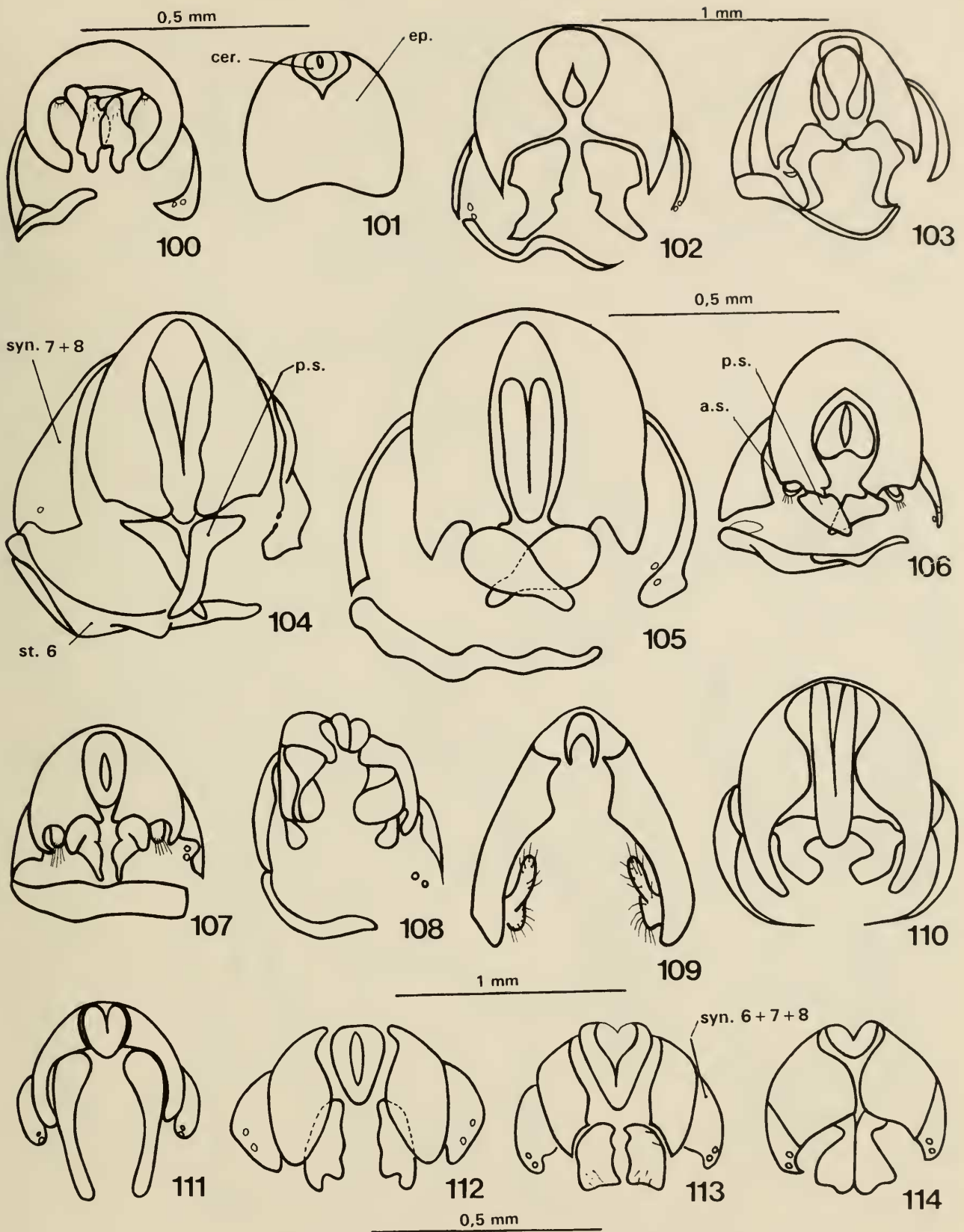
Poecilographa, *Pherbecta* + *Protodictya*. Within the latter group the genera *Limnia*, *Poecilographa*, *Pherbecta* + *Protodictya* are monophyletic. In the third group, which comprises the last fifteen genera, we recognize two subgroups. One is formed by *Hedria*, *Dichetophora*, *Coremacera*, *Dicthyacium*, and *Euthycera*, and the other by *Ethiolimnia*, *Teutoniomyia*, *Thecomyia*, *Sepedoninus*, *Sepedonella*, and *Sepedomerus* + *Sepedonea*. The monophyly of the first



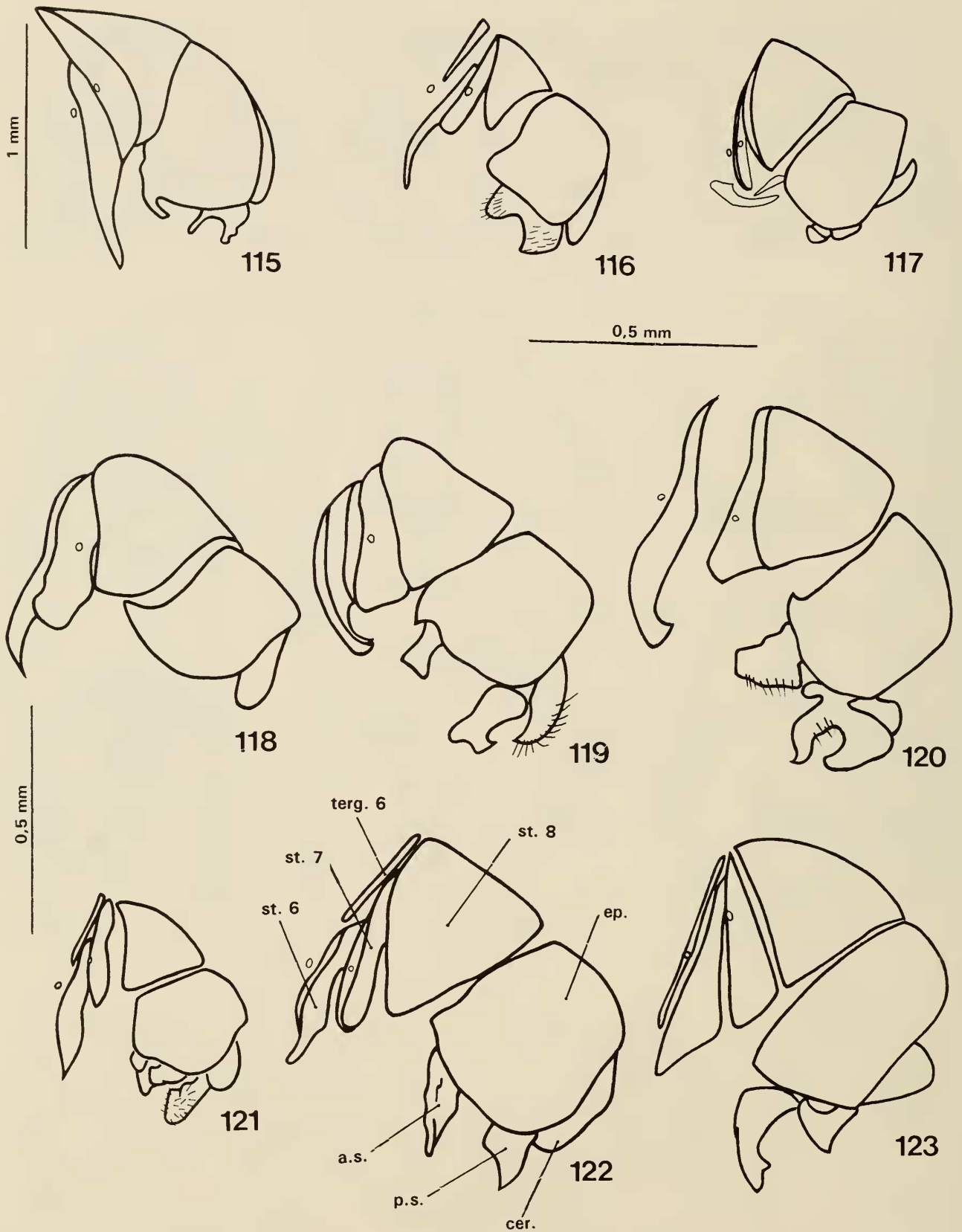
Figs. 77–87. Male terminalia, ventral view: 77, *Ectinocera*; 78, *Renocera*; 79, *Antichaeta*; 80, *Chasmacryptum*; 81, *Shannonia*; 82, *Perilimnia*; 83, *Hoplodictya*; 84, *Dictya*; 85, *Hydromya*; 86, *Neolimnia*; 87, *Euthycerina*. Cerci (cer.); epandrium (ep.); sternite 6 (st. 6); sternite 7 (st. 7); sternite 8 (st. 8); synsternite 7+8 (syn. 7+8); synsternite 6+7+8 (syn. 6+7+8); anterior surstylus (a. s.); posterior surstylus (p. s.). Fig. 86 with scale 1.0 mm; the remaining Figs. with scale 0.5 mm.



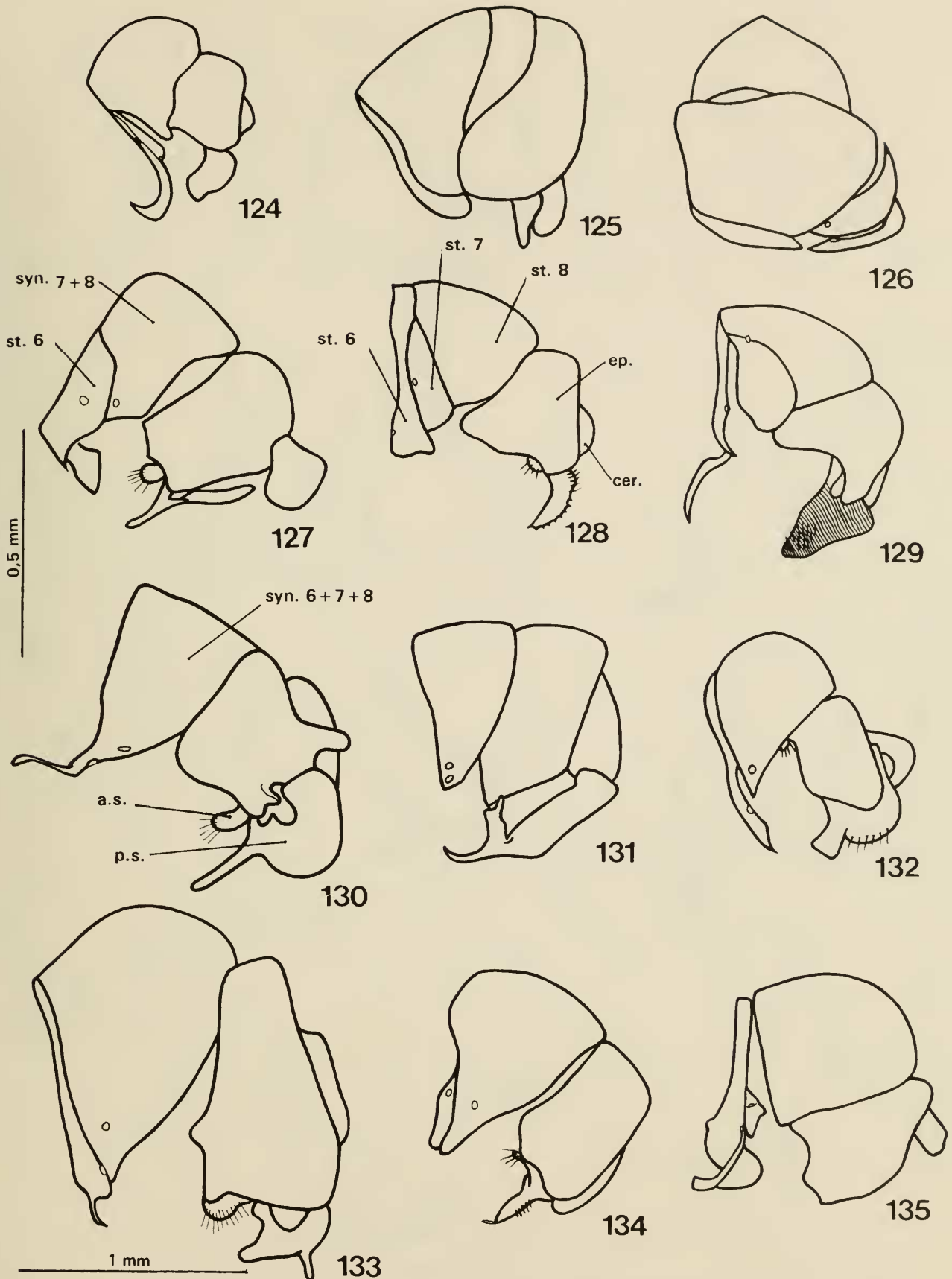
Figs. 88–99. Male terminalia, ventral view: 88, *Tetanocera*; 89, *Trypetolimnia*; 90, *Psacadina*; 91, *Steyskalina*; 92, *Dictyodes*; 93, *Ilione*; 94, *Pherbina*; 95, *Trypetoptera*; 96, *Limnia*; 97, *Poecilographa*; 98, *Pherbecta*; 99, *Protodictya*. Cerci (cer.); epandrium (ep.); sternite 6 (st. 6); synsternite 7+8 (syn. 7+8); synsternite 6+7+8 (syn. 6+7+8); anterior surstylus (a. s.); posterior surstylus (p. s.). Figs. 90 and 98 with scale 0.5 mm; the remaining Figs. with scale 1.0 mm.



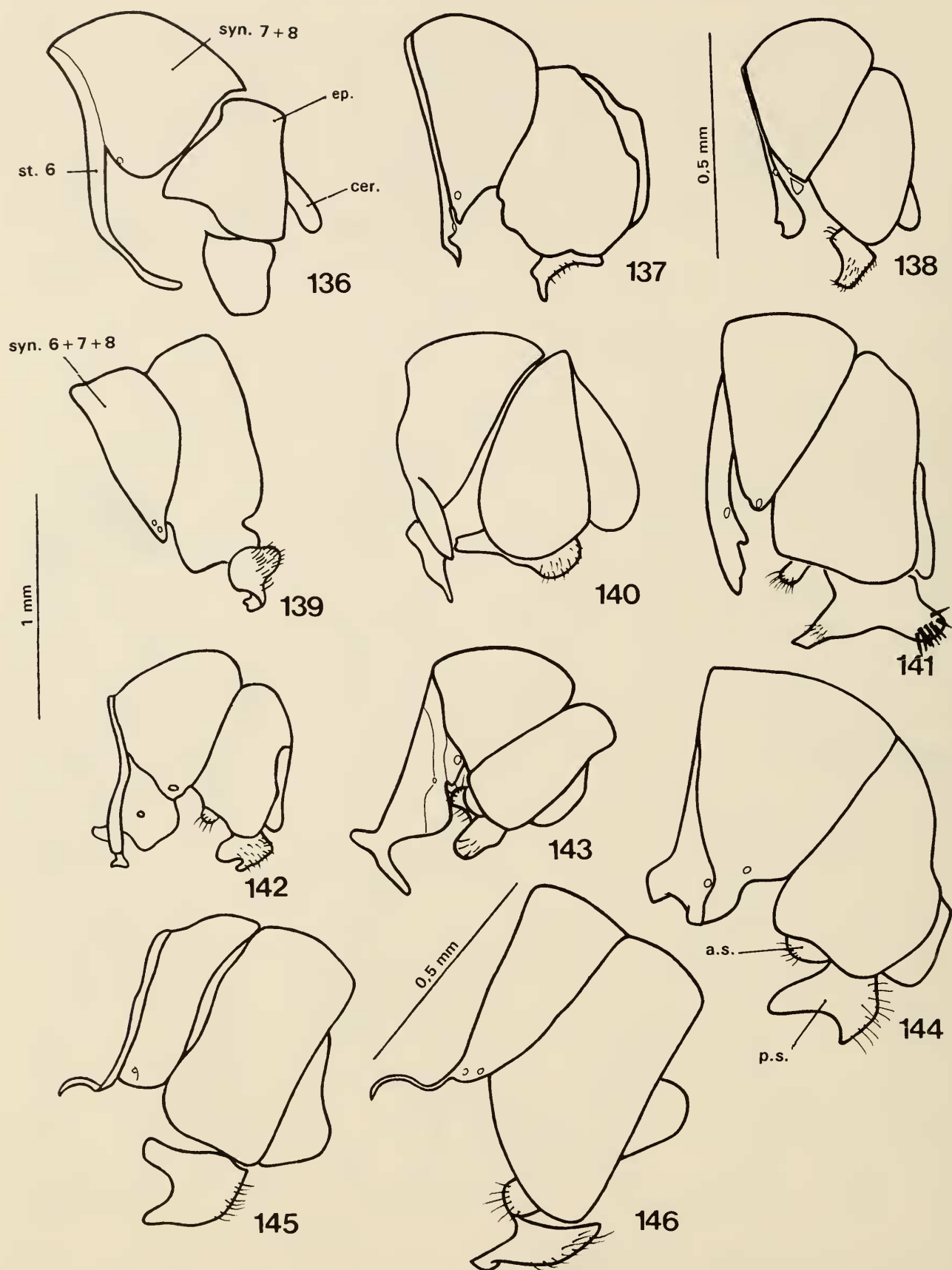
Figs. 100–114. Male terminalia, ventral view: 100–101, *Guatemalaia*; 102, *Elgiva*; 103, *Hedria*; 104, *Diche-tophora*; 105, *Coremacera*; 106, *Dictyaciium*; 107, *Euthycera*; 108, *Ethiolimnia*; 109, *Thecomyia*; 110, *Sepedoninus*; 111, *Sepedonella*; 112, *Sepedon*; 113, *Sepedomerus*; 114, *Sepedonea*. Cerci (cer.); epandrium (ep.); sternite 6 (st. 6); synsternite 7+8 (syn. 7+8); synsternite 6+7+8 (syn. 6+7+8); anterior surstylus (a. s.); posterior surstylus (p. s.). Figs. 100, 101, 104–106, 111–114 with scale 0.5 mm; the remaining Figs. with scale 1.0 mm.



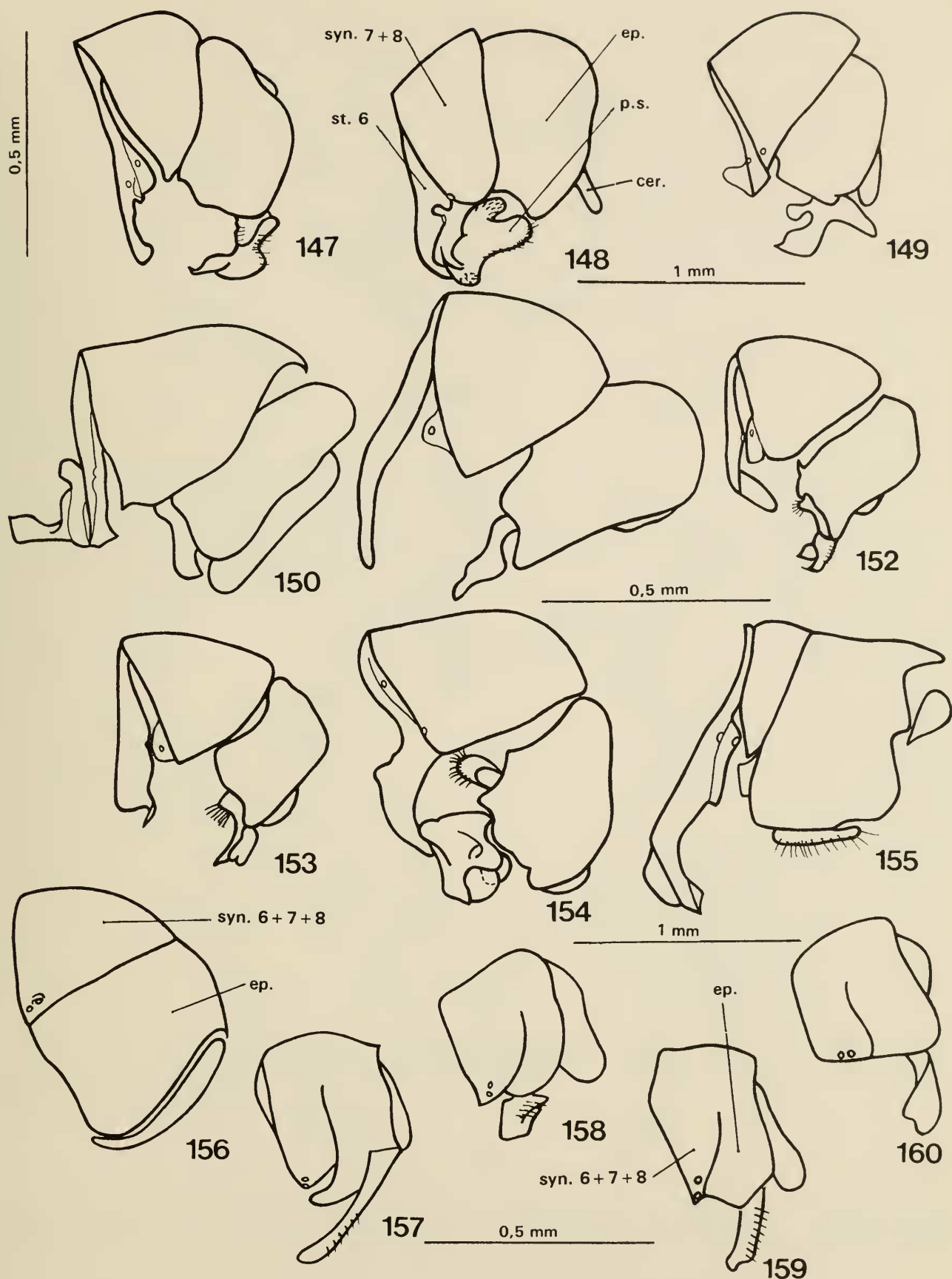
Figs. 115–123. Male terminalia, left lateral view: 115, *Sciomyza*; 116, *Oidematops*; 117, *Atrichomelina*; 118, *Tetanura*; 119, *Colobaea*; 120, *Calliscia*; 121, *Parectinocera*; 122, *Pteromicra*; 123, *Pherbellia*. Cerci (cer.); epandrium (ep.); sternite 6 (st. 6); sternite 7 (st. 7); sternite 8 (st. 8); anterior surstylus (a. s.); posterior surstylus (p. s.); tergite 6 (terg. 6). Fig. 115 with scale 1.0 mm; the remaining Figs. with scale 0.5 mm.



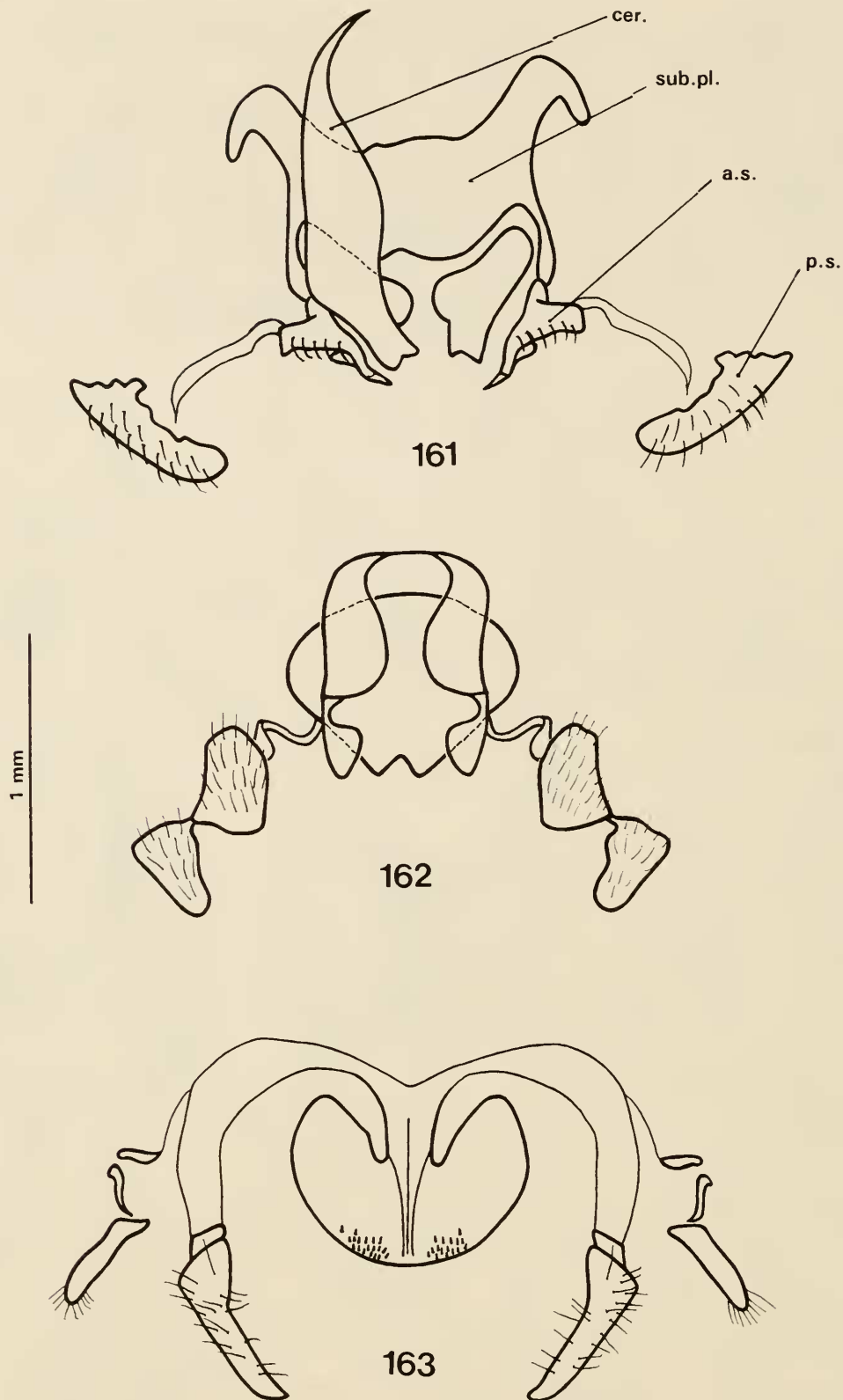
Figs. 124–135. Male terminalia, left lateral view: 124, *Ectinocera*; 125, *Renocera*; 126, *Antichaeta*; 127, *Chasmacryptum*; 128, *Shannonia*; 129, *Perilimnia*; 130, *Hoplodictya*; 131, *Dictya*; 132, *Hydromya*; 133, *Neolimnia*; 134, *Euthycerina*; 135, *Tetanocera*. Cerci (cer.); epandrium (ep.); sternite 6 (st. 6); synsternite 7+8 (syn. 7+8); synsternite 6+7+8 (syn. 6+7+8); anterior surstylus (a. s.); posterior surstylus (p. s.). Figs. 133 with scale 1.0 mm; the remaining Figs. with scale 0.5 mm.



Figs. 136–146. Male terminalia, left lateral view: 136, *Trypetolimnia*; 137, *Psacadina*; 138, *Steyskalina*; 139, *Dictyodes*; 140, *Ilione*; 141, *Pherbina*; 142, *Trypetoptera*; 143, *Limnia*; 144, *Poecilographa*; 145, *Pherbecta*; 146, *Protodictya*. Cerci (cer.); epandrium (ep.); sternite 6 (st. 6); synsternite 7+8 (syn. 7+8); synsternite 6+7+8 (syn. 6+7+8); anterior surstylus (a. s.); posterior surstylus (p. s.). Figs. 138 and 146 with scale 0.5 mm; the remaining Figs. with scale 1.0 mm.



Figs. 147–160. Male terminalia, left lateral view: 147, *Guatemalaia*; 148, *Elgiva*; 149, *Hedria*; 150, *Dichetophora*; 151, *Coremacera*; 152, *Dictyacium*; 153, *Euthycera*; 154, *Ethiolimnia*; 155, *Thecomyia*; 156, *Sepedoninus*; 157, *Sepedonella*; 158, *Sepedon*; 159, *Sepedomerus*; 160, *Sepedonea*. Cerci (cer.); epandrium (ep.); sternite 6 (st. 6); synsternite 7+8 (syn. 7+8); synsternite 6+7+8 (syn. 6+7+8); posterior surstylus (p. s.). Figs. 148–150, 154, 155 with scale 1.0 mm; the remaining Figs. 0.5 mm.

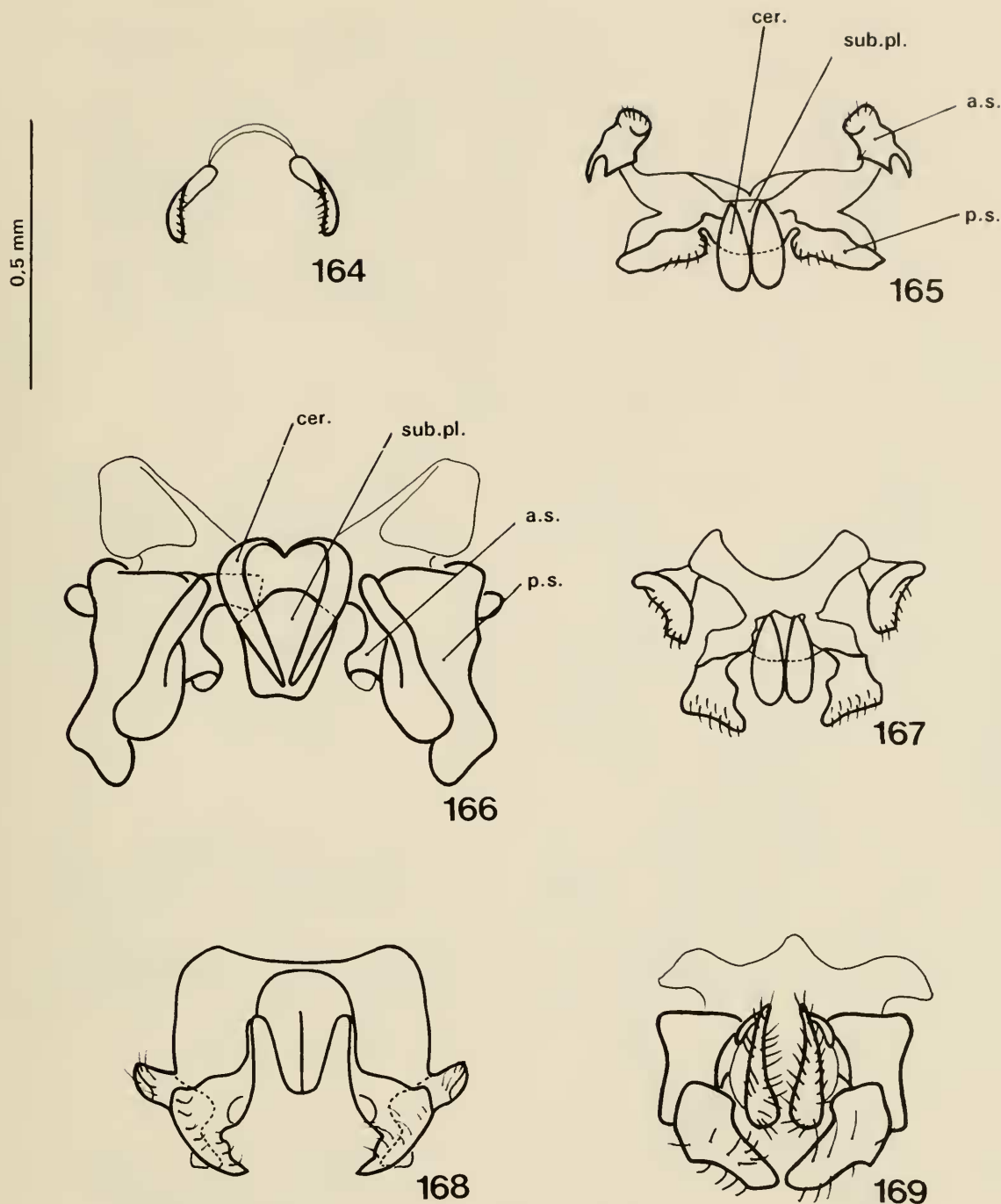


Figs. 161–163. Male terminalia, posterior view: 161, *Sciomyza*; 162, *Oidematops*; 163, *Atrichomelina*. Cerci (cer.); subepandrial plate (sub. pl.); anterior surstylus (a. s.); posterior surstylus (p. s.).

subgroup, from *Thecomyia* to *Sepedonea*, is established by eight characters: 6, 19, 28, 30, 31, 32, 33 and 35. It is the most corroborated lineage within this analysis.

Steyskal (1973) placed *Sepedon* in a

group comprising the genera *Thecomyia*, *Sepedon*, *Sepedonella*, *Sepedoninus*, *Sepedomerus*, and *Sepedonea*. Steyskal (1973: 143) stated that “I do not believe that this group is sufficiently distinct from more typ-



Figs. 164–169. Male terminalia, posterior view: 164, *Tetanura*; 165, *Colobaea*; 166, *Calliscia*; 167, *Parectinocera*; 168, *Pteromicra*; 169, *Pherbellia*. Cerci (cer.); subepandrial plate (sub. pl.); anterior surstylus (a. s.); posterior surstylus (p. s.).

ical Tetanocerini, especially from such genera as *Hedria* and *Dichetophora*, to be given the rank of tribe or even subtribe. We would prefer to call it merely “the *Sepedon* group.” This statement agrees with the result of the present analysis, but with the addition the genera *Ethiolimnia* and *Teutoniomyia* to the *Sepedon* group.

Proposal of classification.—The following natural classification was done using the

sequencing convention (Wiley 1981). The subfamilies Salticellinae and Sciomyzinae and the tribes Sciomyzini and Tetanocerini are confirmed.

Sciomyzidae Fallén, 1820

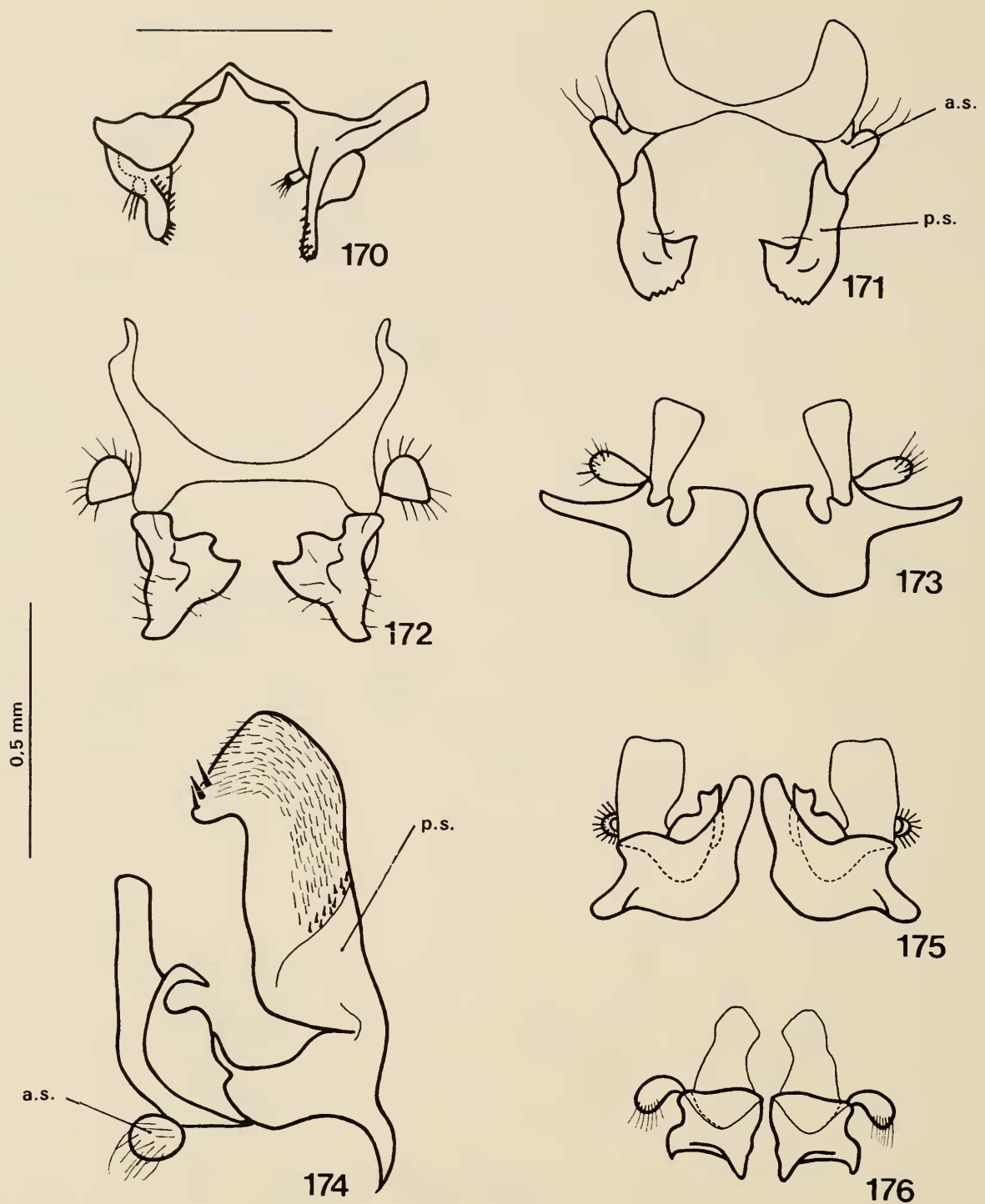
Salticellinae Hendel, 1924

Salticella Robineau-Desvoidy, 1830

Sciomyzinae Fallén, 1820

Sciomyzini Fallén, 1820

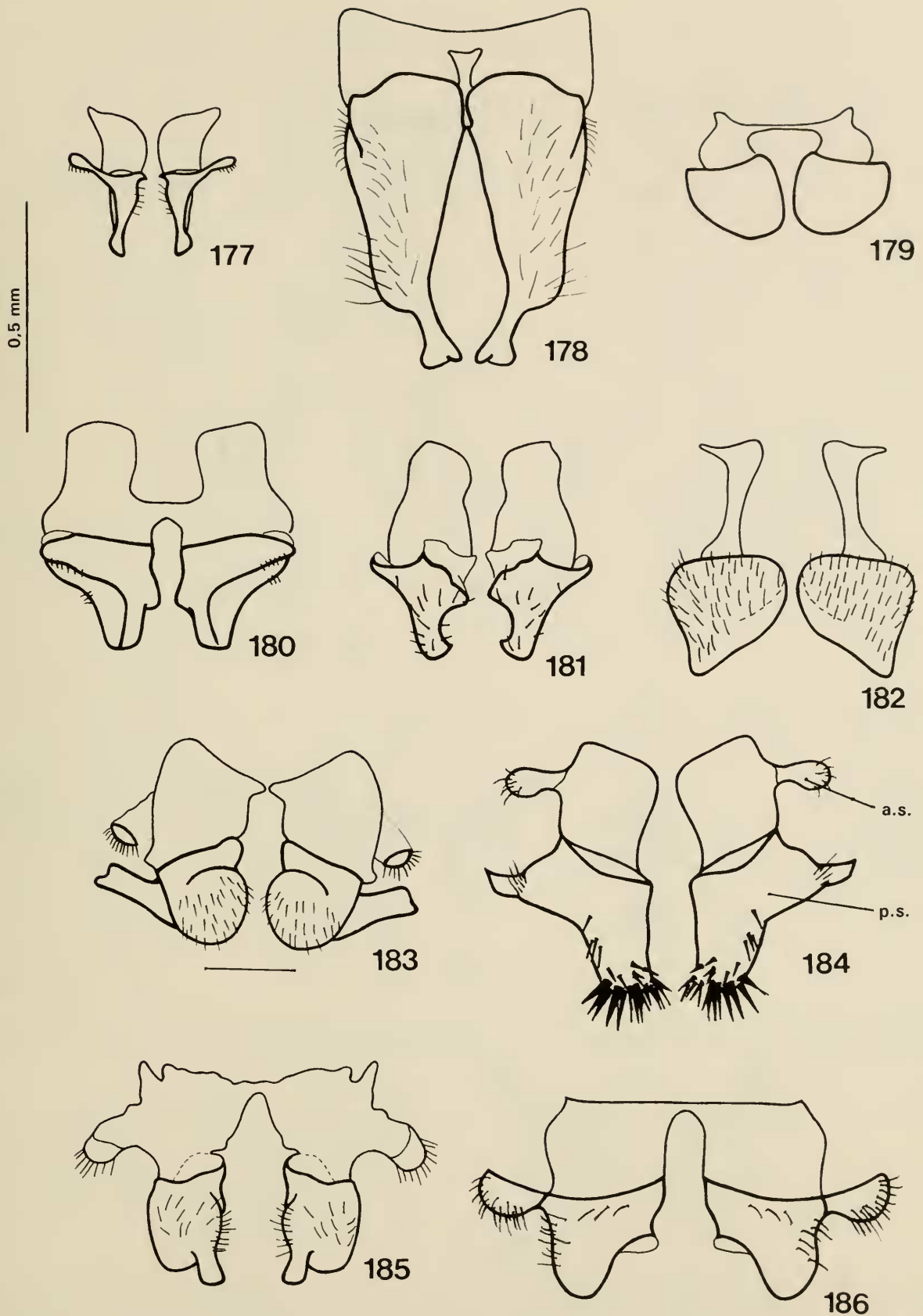
Pherbellia Robineau-Desvoidy, 1830



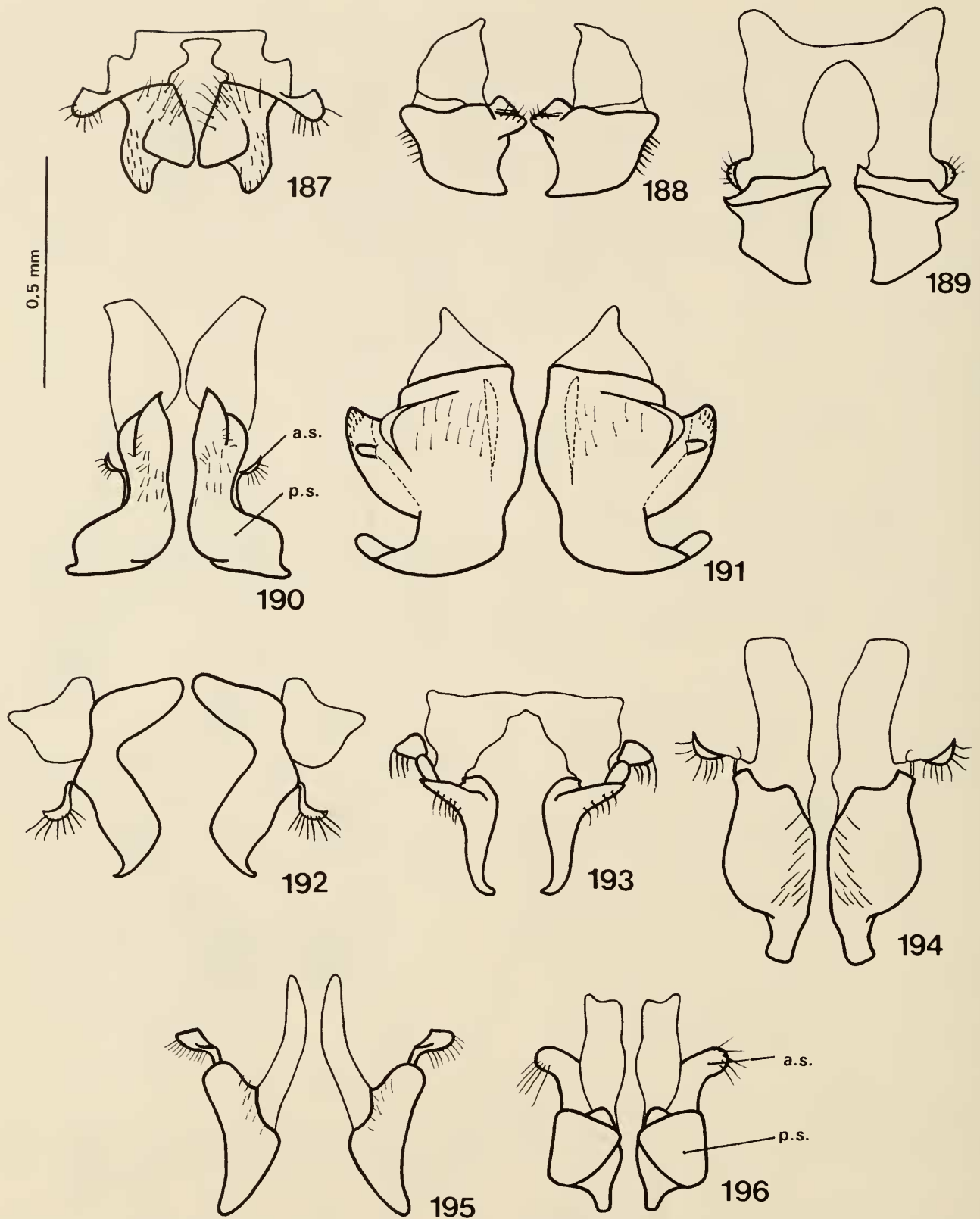
Figs. 170–176. Male terminalia, posterior view: 170, *Antichaeta*; 171, *Shannonia*; 172, *Perilimnia*; 173, *Hoplodictya*; 174, *Dictya* (lateral view), 175, *Hydromya*; 176, *Neolimnia*. Anterior surstylus (a. s.); posterior surstylus (p. s.).

Pteromicra Lioy, 1864
Calliscia Steyskal, 1975
Parectinocera Becker, 1919
Colobaea Zetterstedt, 1837
Tetanura Fallén, 1820
Atrichomelina Cresson, 1920
Oidematops Cresson, 1920
Sciomyza Fallén, 1820
Tetanocerini Hendel, 1900

Eutrichomelina Steyskal, 1975
Ectinocera Zetterstedt, 1838
Renocera Hendel, 1900
Antichaeta Haliday, 1838
Chasmacryptum Becker, 1907
Shannonia Malloch, 1933
Perilimnia Becker, 1919
Hoplodictya Cresson, 1920
Dictya Meigen, 1803



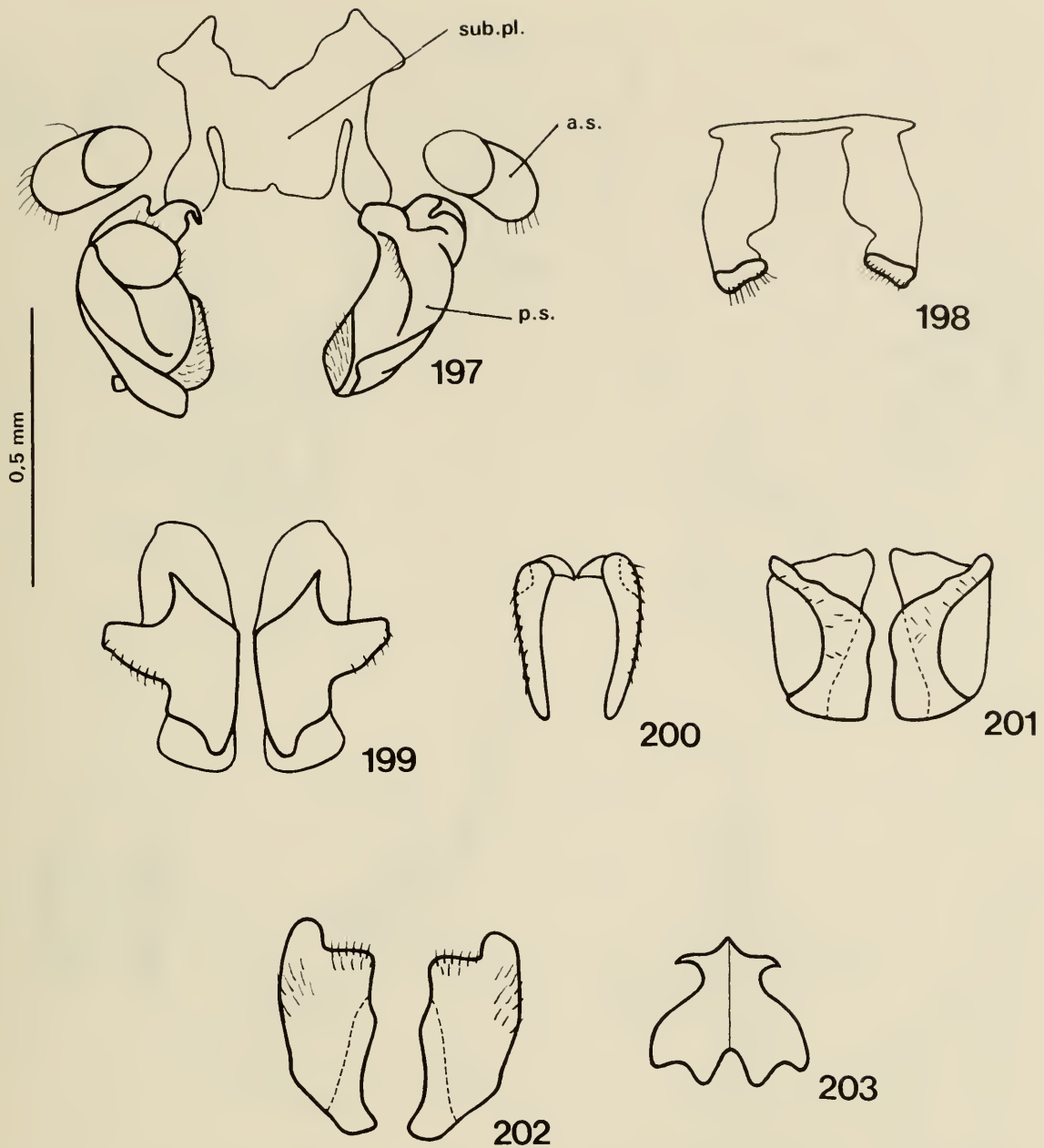
Figs. 177–186. Male terminalia, posterior view: 177, *Euthycerina*; 178, *Tetanocera*; 179, *Trypetolimnia*; 180, *Psacadina*; 181, *Steyskalina*; 182, *Dictyodes*; 183, *Ilione*; 184, *Pherbina*; 185, *Trypetoptera*; 186, *Limnia*. Anterior surstylus (a. s.); posterior surstylus (p. s.).



Figs. 187–196. Male terminalia, posterior view: 187, *Pocilograpta*; 188, *Pherbecta*; 189, *Protodictya*; 190, *Guatemalaia*; 191, *Elgiva*; 192, *Hedria*; 193, *Dichetophora*; 194, *Coremacera*; 195, *Dictyacium*; 196, *Euthycera*. Anterior surstylus (a. s.); posterior surstylus (p. s.).

Hydromya Robineau-Desvoidy, 1830
Neolimnia Barnes, 1976
Tetanoceroides Malloch, 1933
Euthycerina Malloch, 1933

Tetanocera Duméril, 1800
Trypetolimnia Mayer, 1953
Psacadina Enderlein, 1939
Dictyodes Malloch, 1933



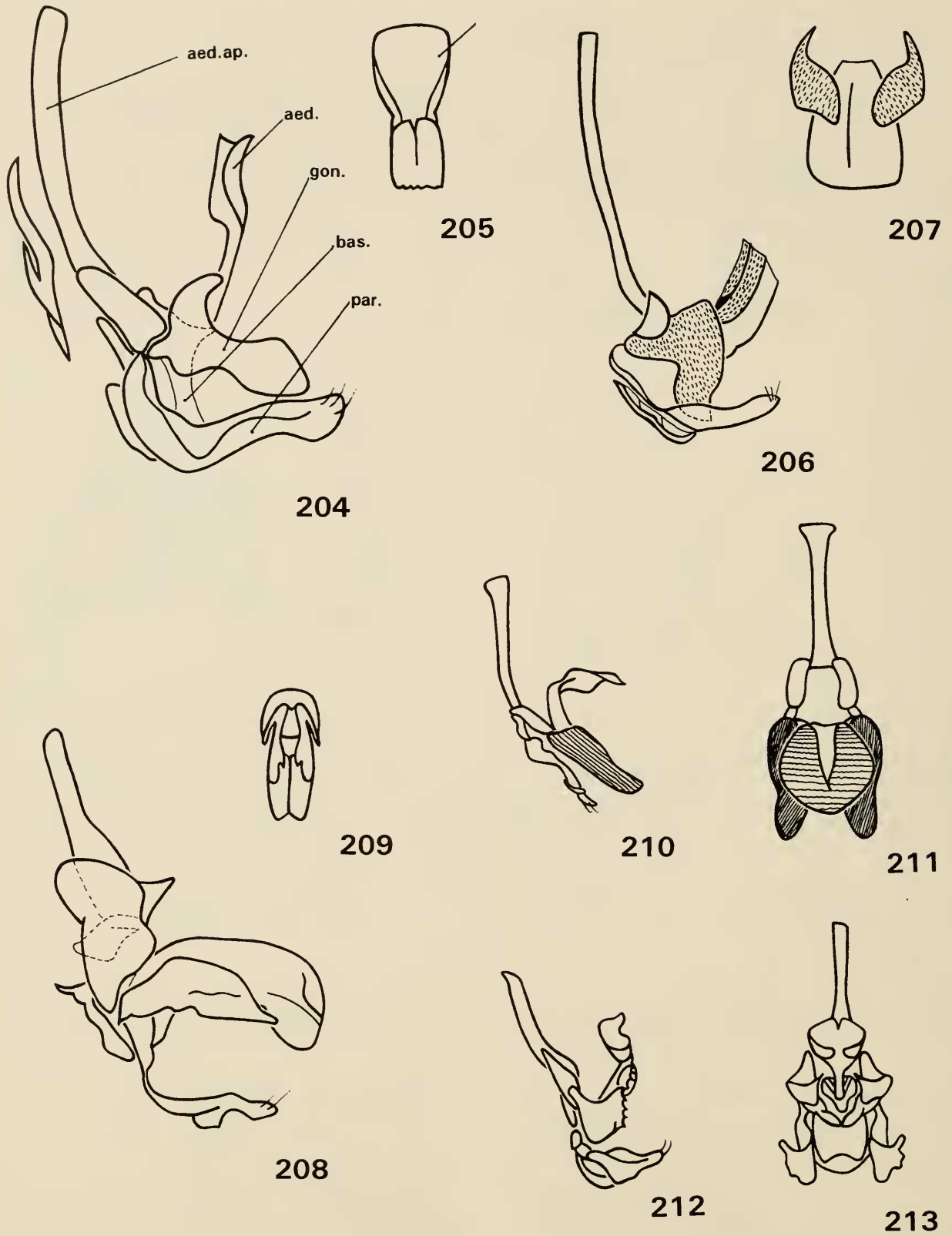
Figs. 197–203. Male terminalia, posterior view: 197, *Ethiolimnia*; 198, *Thecomyia*; 199, *Sepedoninus*; 200, *Sepedonella*; 201, *Sepedon*; 202, *Sepedomerus*; 203, *Sepedonea*. Anterior surstylus (a. s.); posterior surstylus (p. s.).

Ilione Verbeke, 1964
Pherbina Robineau-Desvoidy, 1830
Trypetoptera Hendel, 1900
Limnia Robineau-Desvoidy, 1830
Poecilographa Melander, 1913
Pherbecta Steyskal, 1956
Protodictya Malloch, 1933
Guatemala Steyskal, 1960
Elgiva Meigen, 1838
Hedria Steyskal, 1954
Dichetophora Rondani, 1868
Coremacera Rondani, 1856
Dictyacium Steyskal, 1920
Euthycera Latreille, 1829

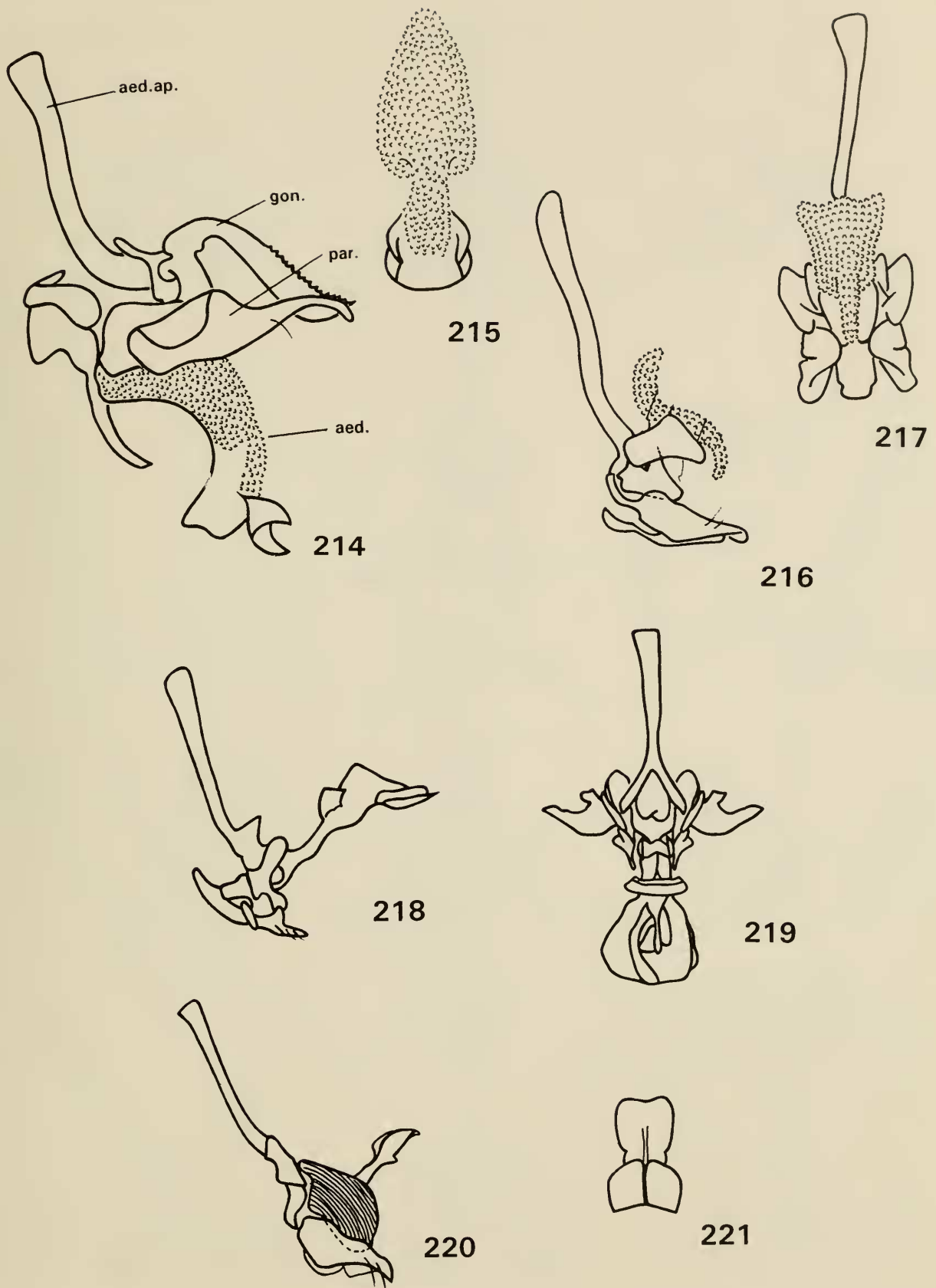
Ethiolimnia Verbeke, 1950
Teutoniomyia Hennig, 1952
Thecomyia Perty, 1833
Sepedoninus Verbeke, 1950
Sepedonella Verbeke, 1950
Sepedon Latreille, 1804
Sepedomerus Steyskal, 1973
Sepedonea Steyskal, 1973
Steyskalina Knutson, 1999

Conclusions

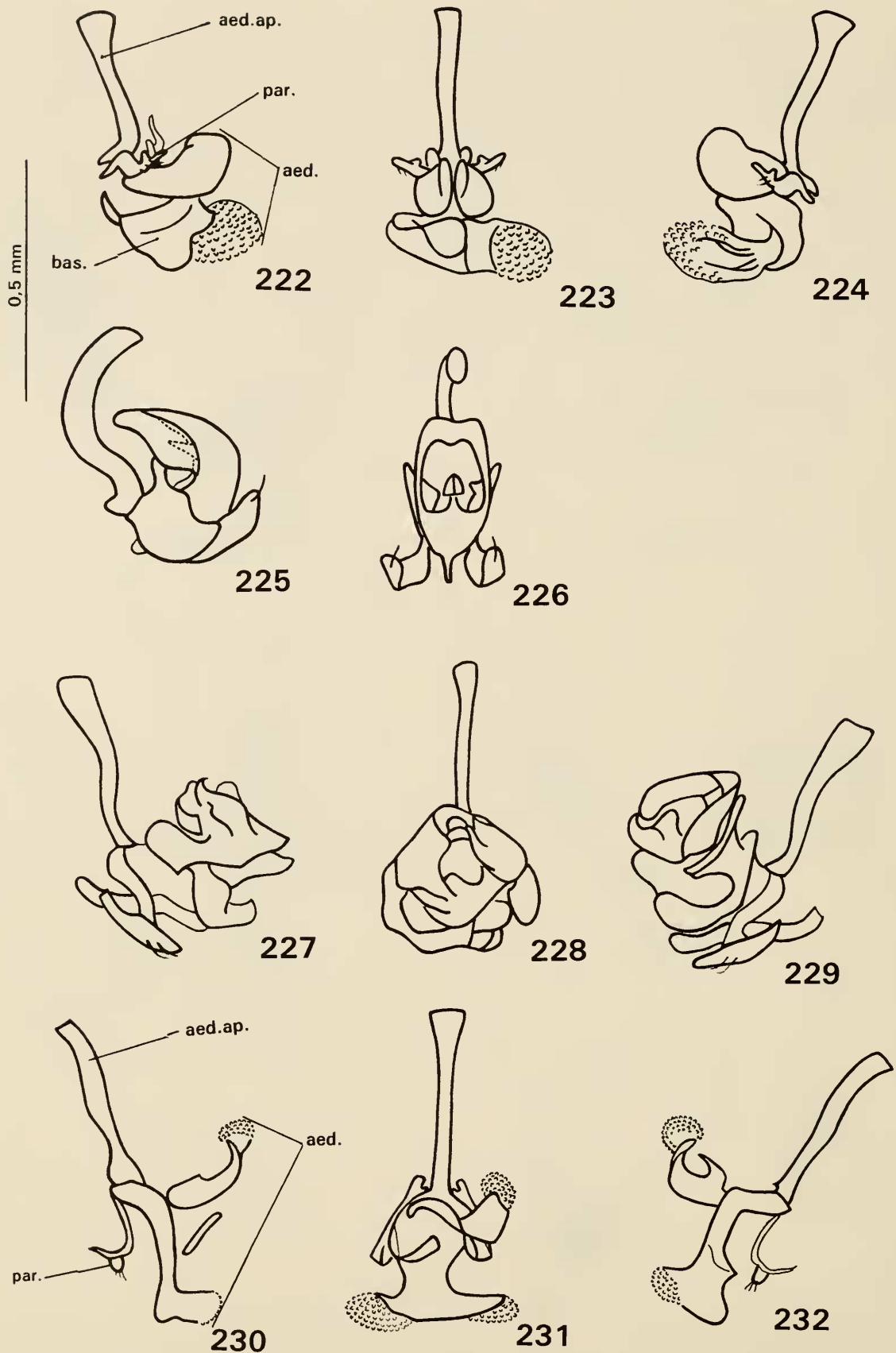
The subfamilies Salticellinae and Sciomyzinae are monophyletic. In the Sciomy-



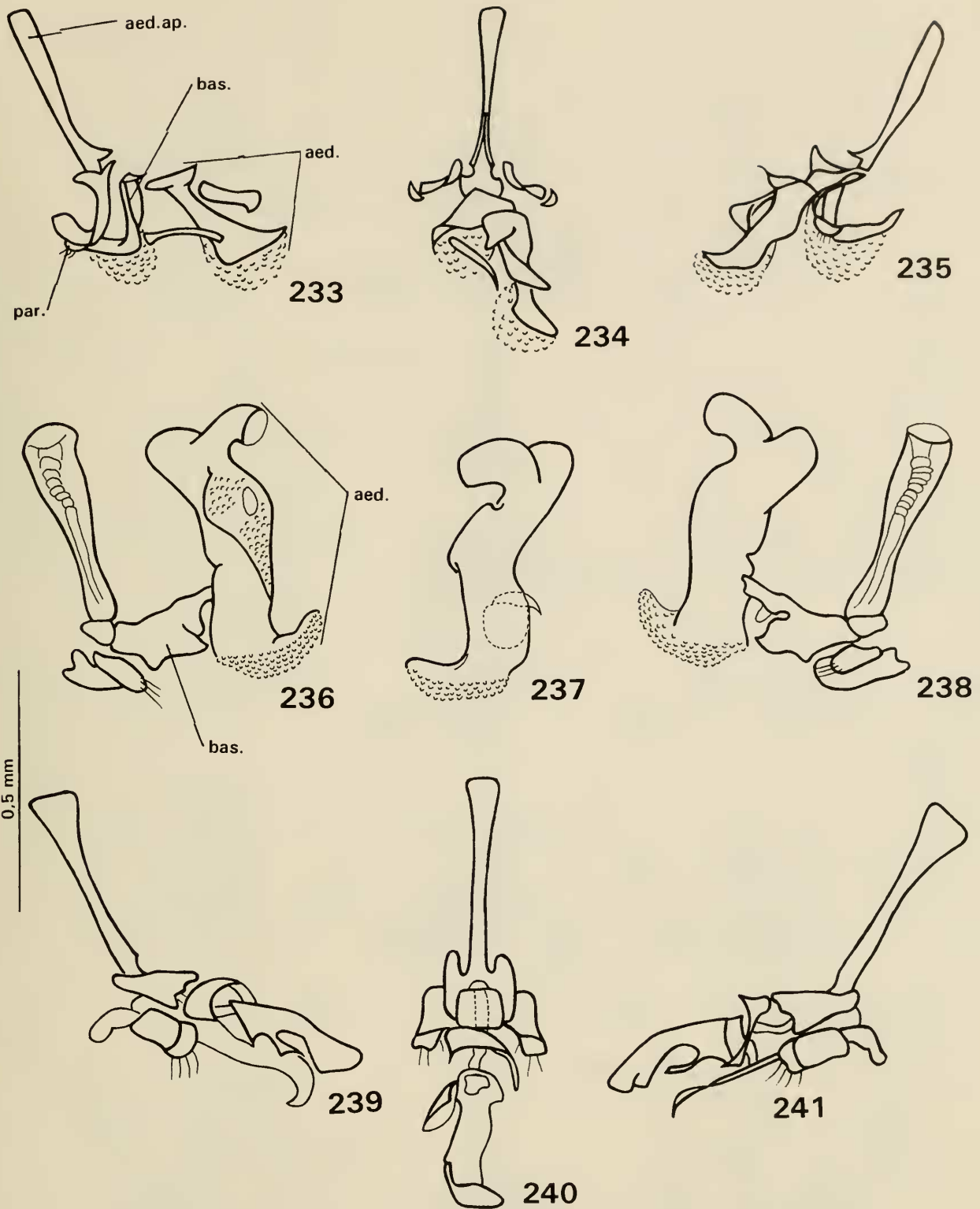
Figs. 204–213. Male terminalia. 204, 208, 206, 210, 212, Right lateral view; 205, 207, 209, 211, 213, frontal view. 204, 205, *Sciomyza*; 206, 207, *Oidematops*; 208–209, *Atrichomelina*; 210–211, *Tetanura*; 212–213, *Colobaea*. Aedeagal apodeme (aed. ap.); basiphallus (bas.); aedeagus (aed.); gonopod (gon.); hypandrium (hip.); paramere (par.).



Figs. 214–221. Male terminalia. 214, 216, 218, 220, Right lateral view; 215, 217, 219, 221, frontal view. 214, 215, *Calliscia*; 216, 217, *Parectinocera*; 218, 219, *Pteromicra*; 220, 221, *Pherbellia*. Aedeagal apodeme (aed. ap.); basiphallus (bas.); aedeagus (aed.); gonopod (gon.); hypandrium (hip.); paramere (par.).



Figs. 222-232. Male terminalia. 222, 225, 227, 230, Right lateral view; 223, 226, 228, 231, frontal view; 224, 229, 232, left lateral view. 222-224, *Ectinocera*; 225-226, *Antichaeta*; 227-229, *Chasmacryptum*; 230-232, *Shannonia*. Aedeagal apodeme (aed. ap.); basiphallus (bas.); aedeagus (aed.); paramere (par.).

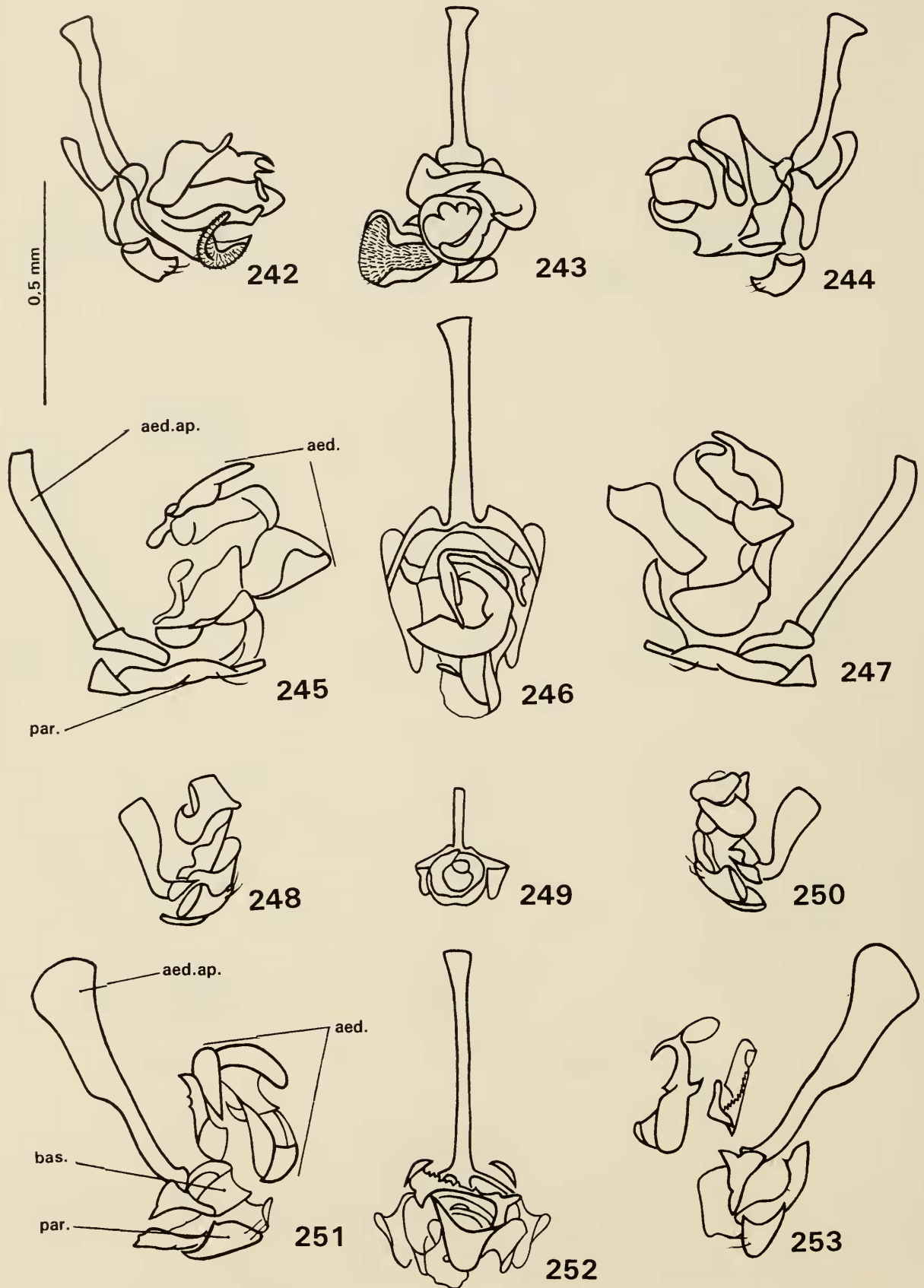


Figs. 233–241. Male terminalia. 233, 236, 239, Right lateral view; 234, 237, 240, frontal view; 235, 238, 241, left lateral view. 233–235, *Perilimnia*; 236–238, *Hoplodictya*; 239–241, *Dictya*. Aedeagal apodeme (aed. ap.); basiphallus (bas.); aedeagus (aed.); paramere (par.).

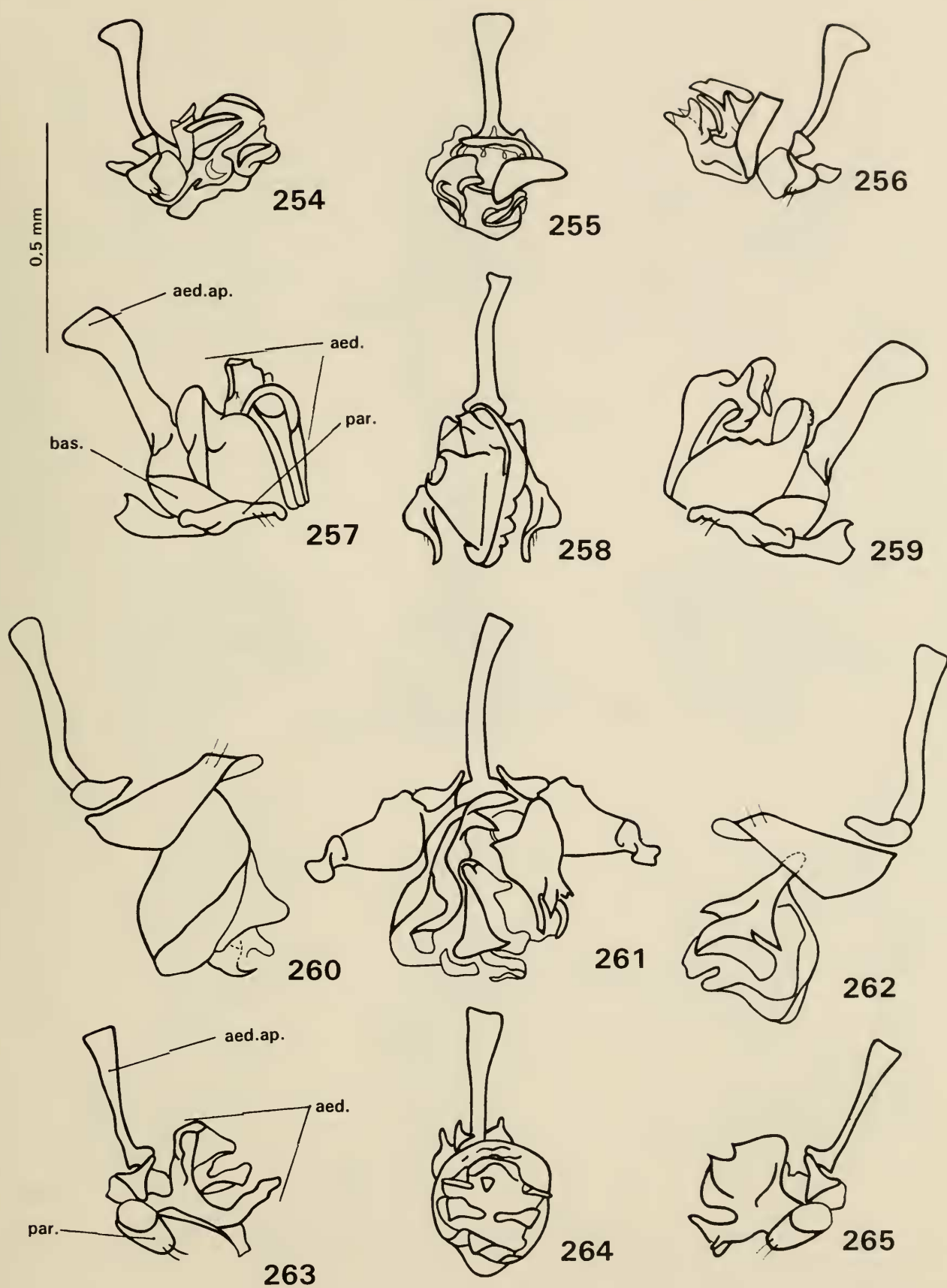
zinae the tribes Sciomyzini and Tetanocerini are monophyletic.

The tribe Sciomyzini includes *Pherbellia*, *Pteromicra*, *Calliscia*, *Parectinocera*, *Colobaea*, *Tetanura*, *Atrichomelina*, *Oidematomops*, and *Sciomyza*.

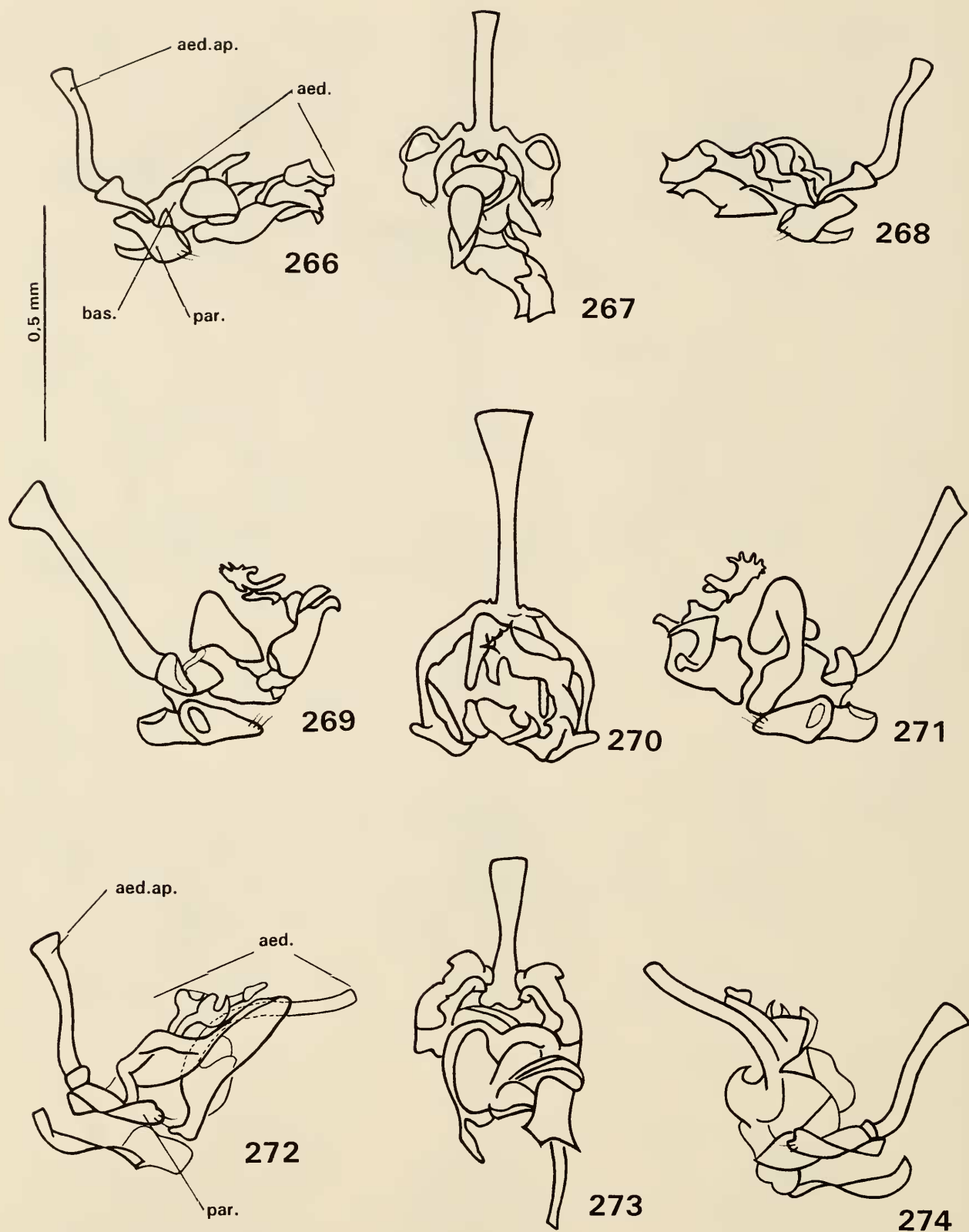
The tribe Tetanocerini includes *Antichaeata*, *Chasmacryptum*, *Coremacera*, *Dichetophora*, *Dictya*, *Dictyacium*, *Dictyodes*, *Ectinocera*, *Elgiva*, *Ethiolimnia*, *Euthycera*, *Euthycerina*, *Eutrichomelina*, *Guatemalaia*, *Hedria*, *Hydromya*, *Hoplodictya*, *Ilione*,



Figs. 242-253. Male terminalia. 242, 245, 248, 251, Right lateral view; 243, 246, 249, 252, frontal view; 244, 247, 250, 253, left lateral view. 242-244, *Hydromya*; 245-247, *Neolimnia*; 248-250, *Euthycerina*; 251-253, *Tetanocera*. Aedeagal apodeme (aed. ap.); aedeagus (aed.); paramere (par.).



Figs. 254–265. Male terminalia. 254, 257, 260, 263, Right lateral view; 255, 258, 261, 264, frontal view; 256, 259, 262, 265, left lateral view. 254–256, *Trypetolimnia*; 257–259, *Psacadina*; 260–262, *Steyskalina*; 263–265, *Dictyodes*. Aedeagal apodeme (aed. ap.); basiphallus (bas.); aedeagus (aed.); paramere (par.).

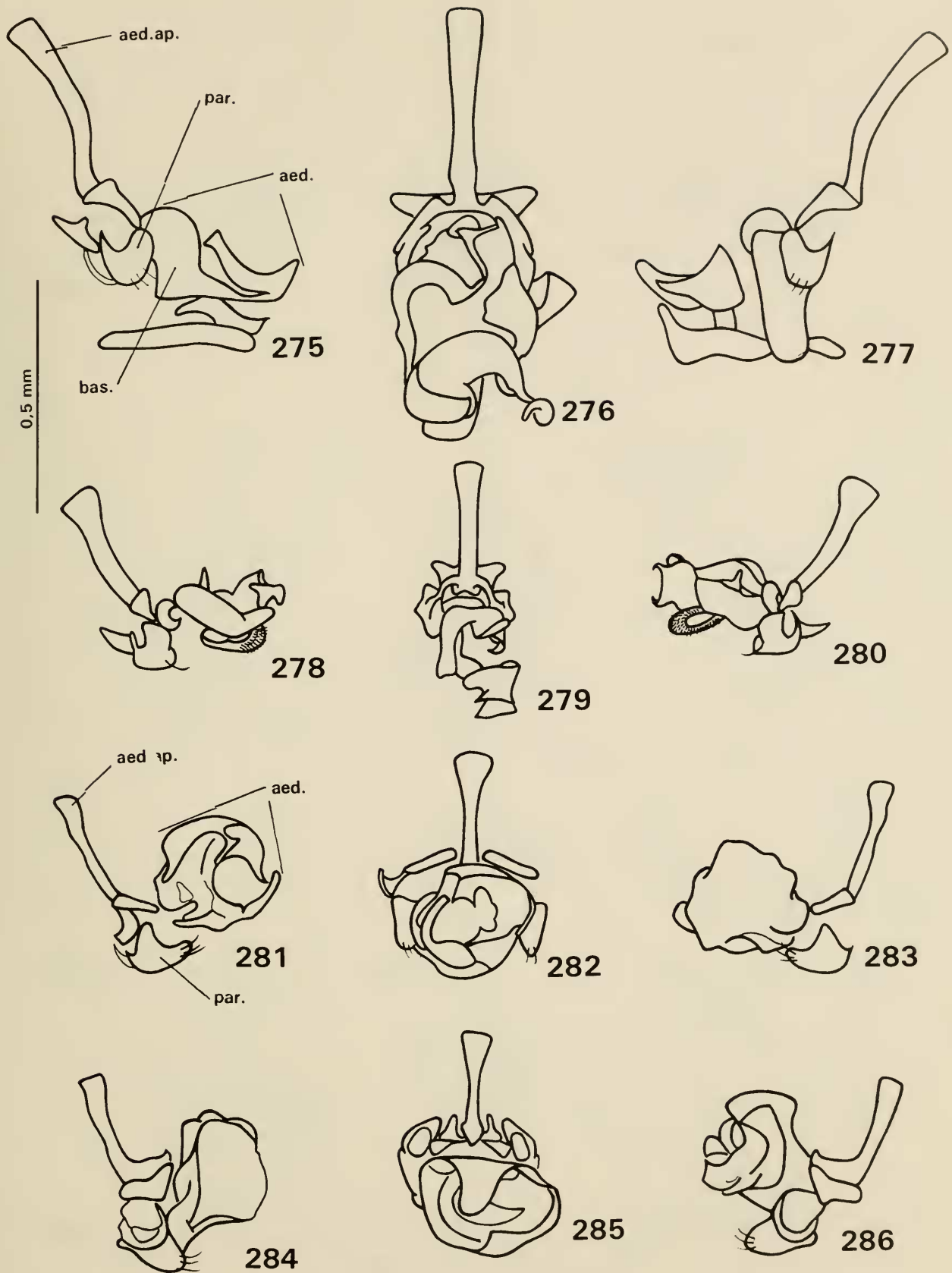


Figs. 266–274. Male terminalia. 266, 269, 272, Right lateral view; 267, 270, 273, frontal view; 268, 271, 274, left lateral view. 266–268, *Ilione*; 269–271, *Pherbina*; 272–274, *Trypetoptera*. Aedeagal apodeme (aed. ap.); basiphallus (bas.); aedeagus (aed.); paramere (par.).

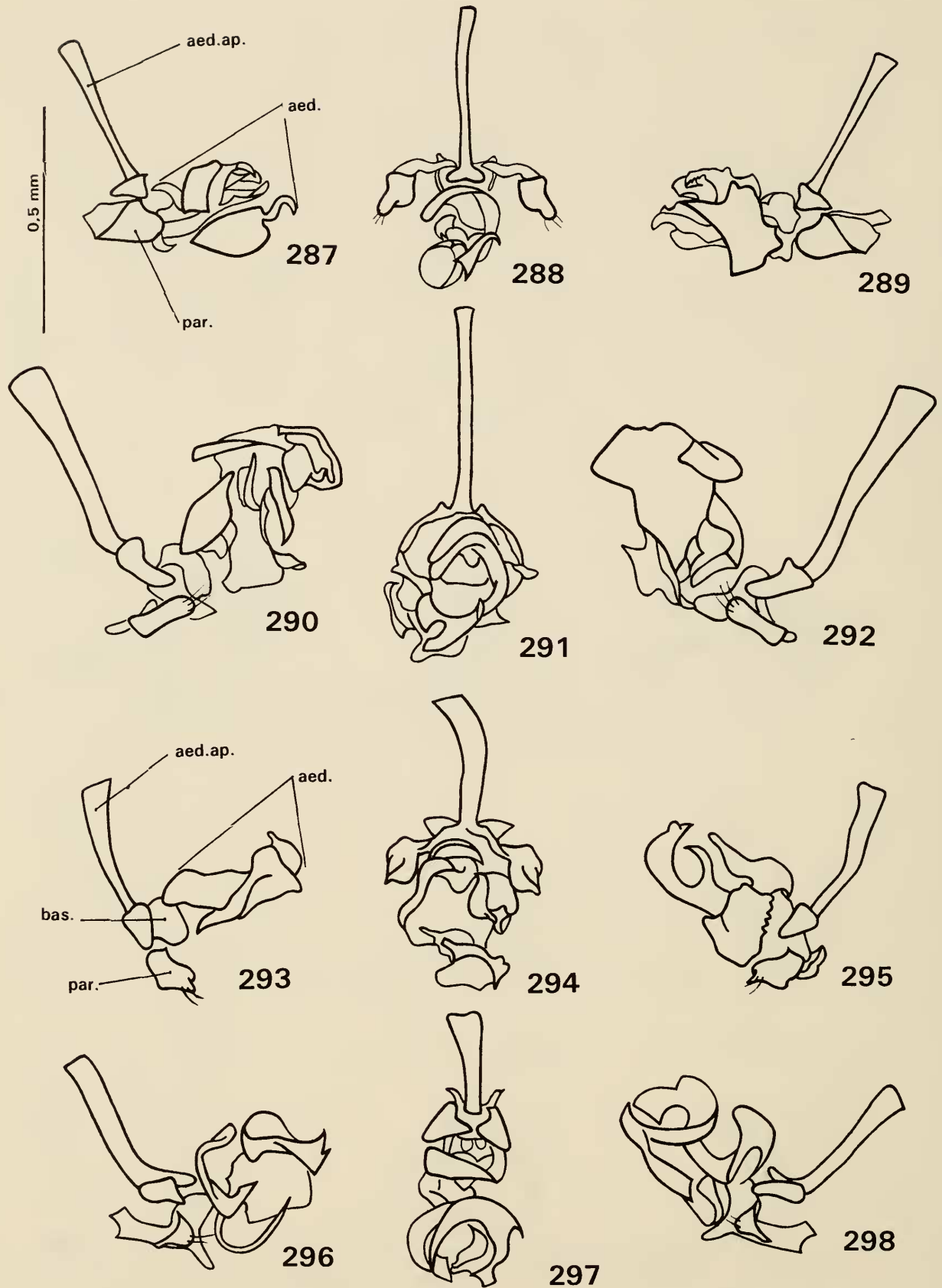
Limnia, *Neolimnia*, *Perilimnia*, *Pherbecta*, *Pherbina*, *Poecilographa*, *Protodictya*, *Psacadina*, *Renocera*, *Sepedoninus*, *Sepedonella*, *Sepedon*, *Sepedomerus*, *Sepedo-*

nea, *Shannonia*, *Steyskalina*, *Tetanocera*, *Tetanoceroides*, *Trypetoptera*, *Trypetolimnia*, *Teutoniomyia*, and *Thecomyia*.

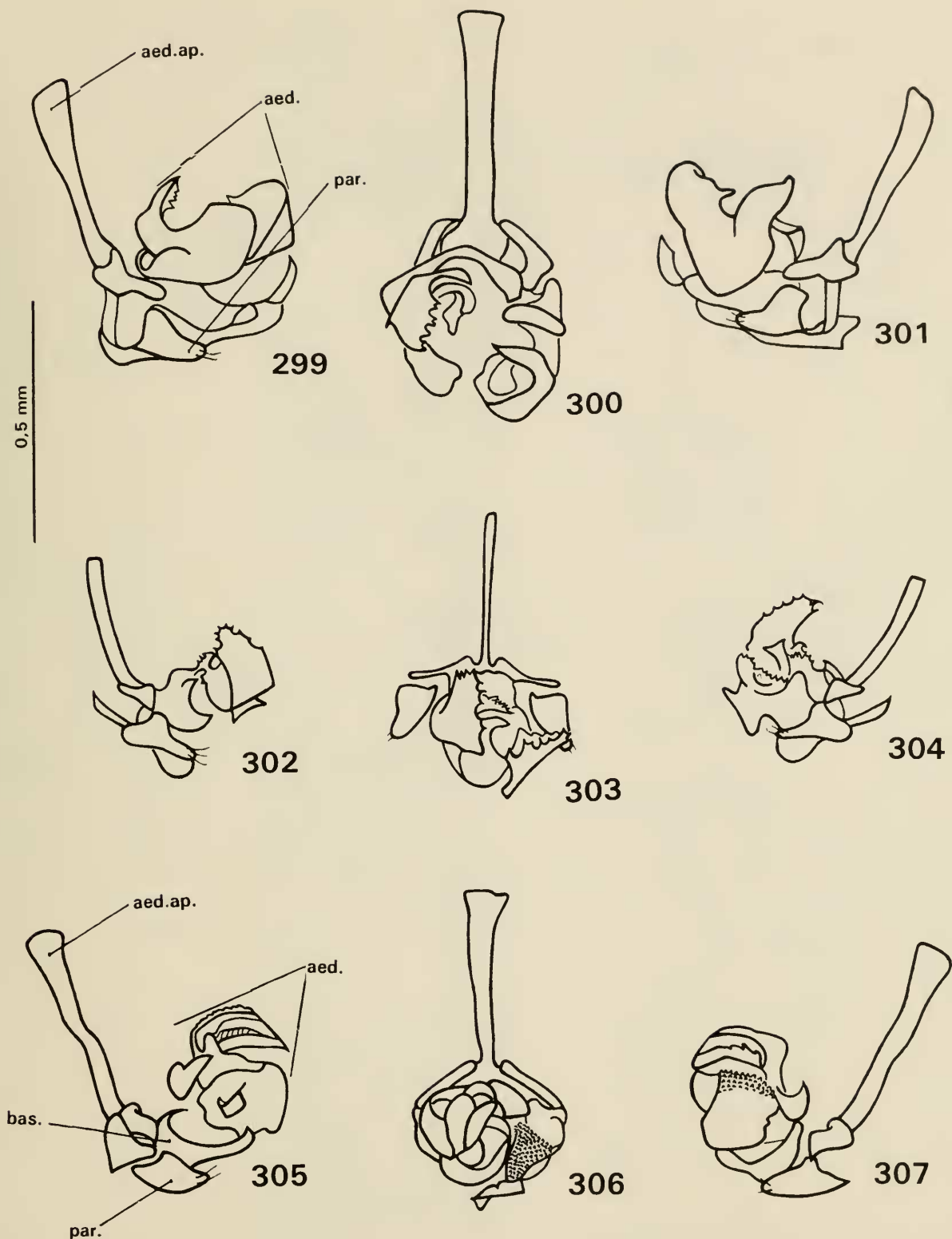
Within the Sciomyzini a monophyletic



Figs. 275–286. Male terminalia. 275, 278, 281, 284, Right lateral view; 276, 279, 282, 285, frontal view; 277, 280, 283, 286, left lateral view. 275–277, *Limnia*; 278–280, *Poecilographa*; 281–283, *Pherbecta*; 284–286, *Protodictya*. Aedeagal apodeme (aed. ap.); aedeagus (aed.); paramere (par.).



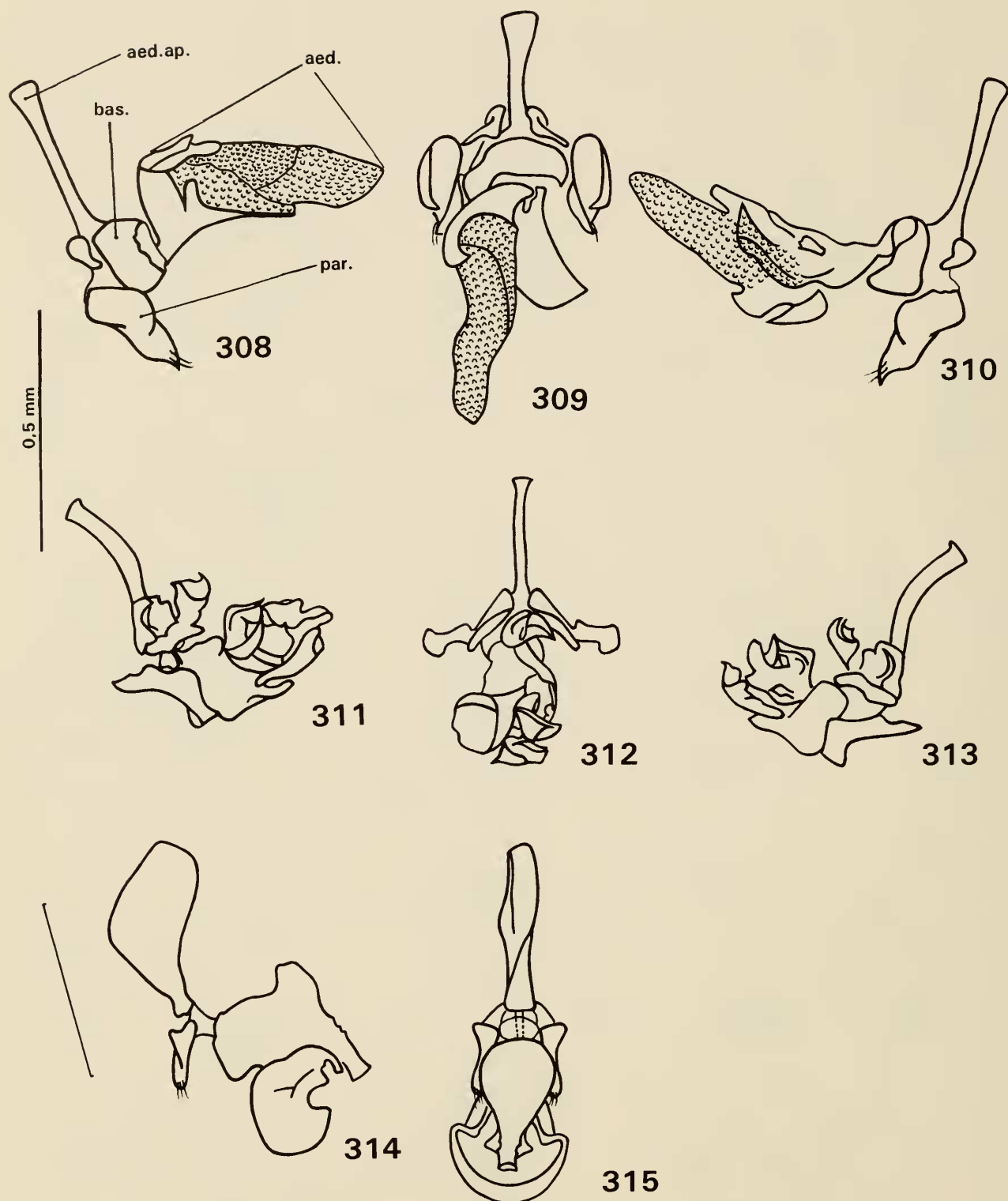
Figs. 287-298. Male terminalia. 287, 290, 293, 296, Right lateral view; 288, 291, 294, 297, frontal view; 289, 292, 295, 298, left lateral view. 287-289, *Guatemalaia*; 290-292, *Elgiva*; 293-295, *Hedria*; 296-298, *Dichetophora*. Aedeagal apodeme (aed. ap.); basiphallus (bas.); aedeagus (aed.); paramere (par.).



Figs. 299-307. Male terminalia. 299, 302, 305, Right lateral view; 300, 303, 305, frontal view; 301, 304, 306, left lateral view. 299-301, *Coremacera*; 302-304, *Dictyacium*; 305-307, *Euthycera*. Aedeagal apodeme (aed. ap.); basiphallus (bas.); aedeagus (aed.); paramere (par.).

group was formed by the genera *Colobaea*, *Tetanura*, *Atrichomelina*, *Oidematops* + *Sciomyza*. In this group there is the subgroup formed by *Atrichomelina*, *Oidematops* + *Sciomyza*.

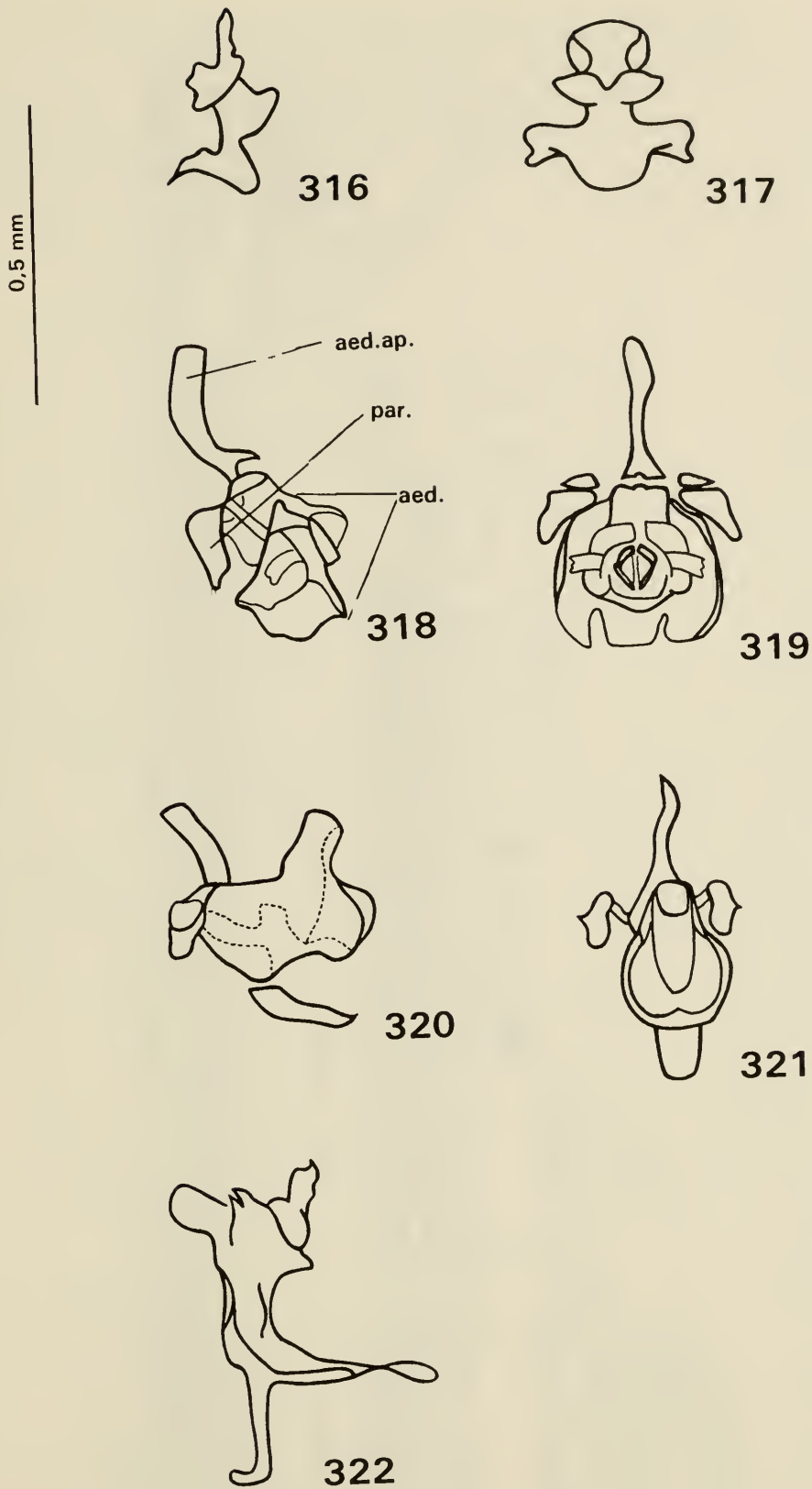
The groups of *Shannonia* + *Perilimnia* and *Hoplodictya* + *Dictya*, at the base of Tetanocerini, are monophyletic. Three other major groups of genera are formed within the Tetanocerini: the first by *Eu-*



Figs. 308–315. Male terminalia. 308, 311, 314, Right lateral view; 309, 312, 315, frontal view; 310, 313, left lateral view. 308–310, *Ethiolimnia*; 311–313, *Thecomyia*; 314, 315, *Sepedoninus*. Aedeagal apodeme (aed. ap.); basiphallus (bas.); aedeagus (aed.); paramere (par.).

thycerina, *Psacadina* Enderlein (1933), *Steyskalina*, *Tetanocera*, and *Trypetolimnia*, the second by the genera *Dictyodes*, *Ilione*, *Pherbina*, *Trypetoptera*, *Limnia*, *Poecilographa*, and *Pherbecta* + *Proto-*

dictya, and the third by *Guatemala*, *Elgiva*, *Dichetophora*, *Hedria*, *Coremacera*, *Dictyacium*, *Euthycera*, *Ethiolimnia*, *Teutoniomyia*, *Thecomyia*, *Sepedoninus*, *Sepedonella*, *Sepedon*, *Sepedomerus* + *Se-*



Figs. 316–322. Male terminalia. 316, 318, 320, 322, Right lateral view; 317, 319, 321, frontal view. 316, 317, *Sepedonella*; 318, 319, *Sepedon*; 320, 321, *Sepedomerus*; 322, *Sepedonea*. Aedeagal apodeme (aed. ap.); aedeagus (aed.); paramere (par.).

pedonea. Within the last group the genera *Coremacera*, *Dictyacium*, and *Euthycera* form a monophyletic clade without any resolution of their phylogenetic relation-

ships; and the group of *Ethiolimnia*, *Teutoniomyia*, *Thecomyia*, *Sepedoninus*, *Sepedonella*, *Sepedon*, *Sepedomerus* + *Sepedonea* is monophyletic.

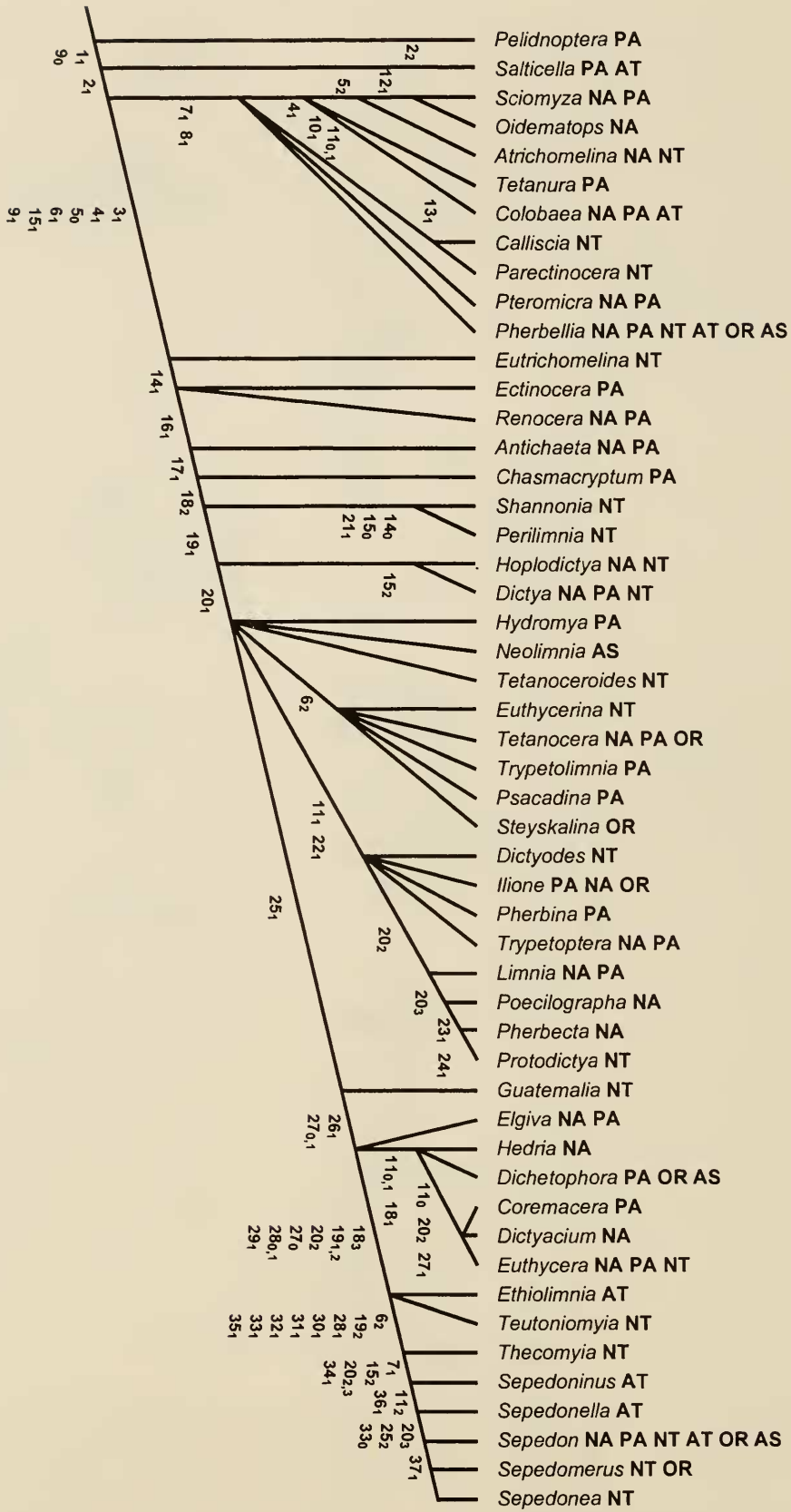


Fig. 323. Consensus cladogram. Outgroup *Pelidnoptera*. 37 characters. Consistency index: 0.60. Retention index: 0.88. Regions: AT, Afrotropical; AS, Australian; NA, Nearctic; NT, Neotropical; OR, Oriental; PA, Palearctic.

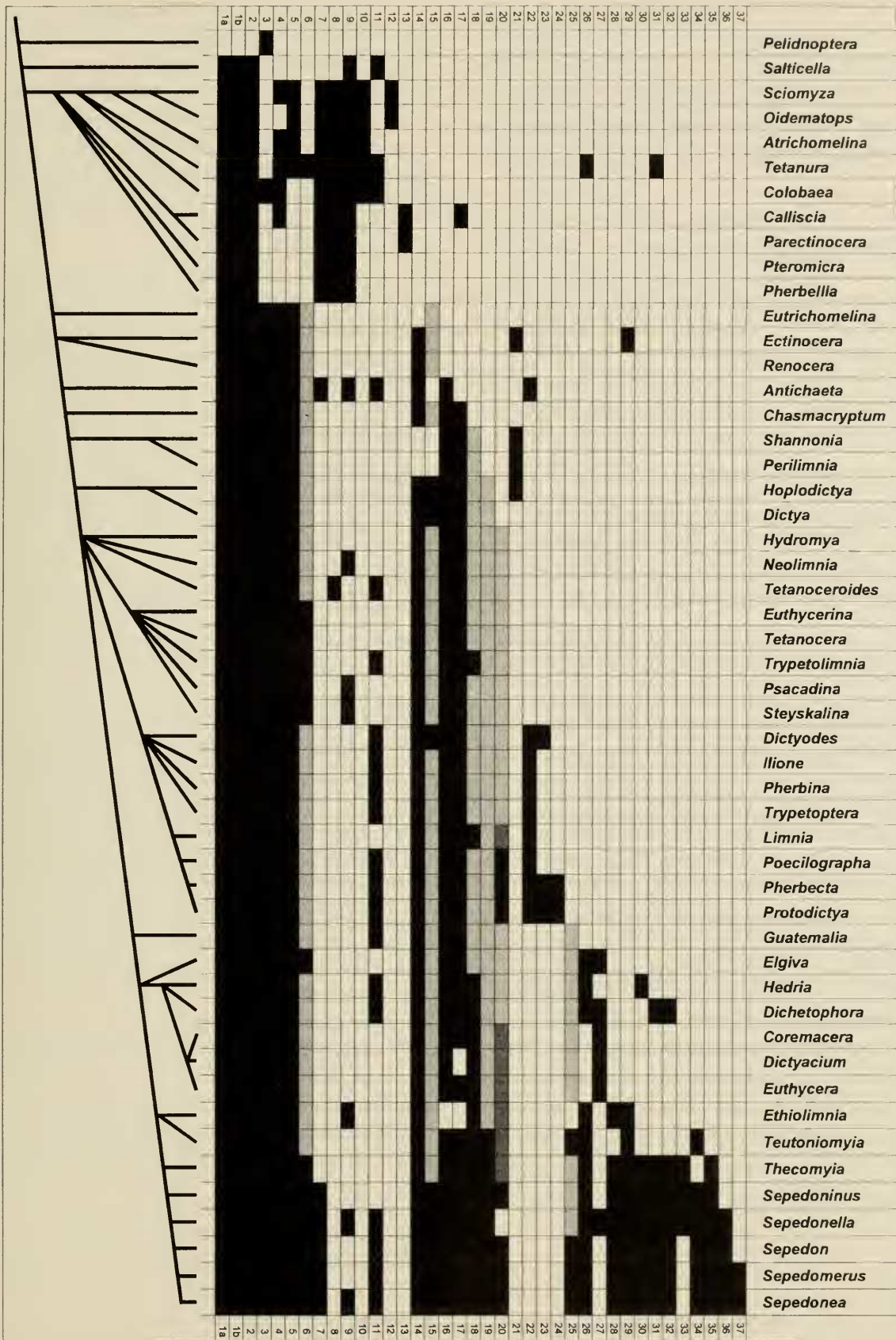


Fig. 324. Arrangement of character states among genera of Sciomyzidae. White = plesiomorphic condition; gray (light and dark) = intermediate and relatively more apomorphic conditions for multistate characters (progressing from light gray to dark gray); black = apomorphic condition.

Acknowledgments

Many individuals and institutions have contributed to this analysis. We thank the following institutions and respective curators for their cooperation in lending specimens.

BMNH	The Natural History Museum, London, England
DZUP	Coleção de Entomologia Pe. J. S. Moure, Department of Zoology, Universidade Federal do Paraná, Curitiba, Paraná, Brazil
INPA	Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil
MNRJ	Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Rio de Janeiro, Brazil
MZSP	Museu de Zoologia da Universidade de São Paulo, São Paulo, São Paulo, Brazil
UCR	University of California, Riverside, California, U.S.A.
USNM	former United States National Museum, collections in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

We thank Dr. Claudio J. B. de Carvalho, Dr^a Marcia S. Couri, Dr^a Dilma S. Napp, & Dr. Angelo P. do Prado for reviewing the manuscript and Dr. John Kingsolver for reviewing the English version. We also thank Drs. Rudolf Rozkošný & Lloyd V. Knutson for very constructive discussions on numerous aspects and the conclusions that are presented in this paper.

Literature Cited

- Abercrombie, J. 1970. Natural history of snail-killing flies of South America (Diptera: Sciomyzidae: Tetanocerini). Unpublished Ph.D. thesis, Cornell University. 344 pp.
- , & C. O. Berg. 1975. Natural history of *Thecomyia limbata* (Diptera: Sciomyzidae) from Brazil.—Proceedings of the Entomological Society of Washington 77:355–368.
- , & ———. 1978. Malacophagous Diptera of South America: biology and immature stages of *Dictyodes* (Sciomyzidae).—Revista Brasileira de Entomologia 22(1):23–32.
- Barnes, J. K. 1979. The taxonomic position of the New Zealand genus *Prosochaeta* Malloch (Diptera: Sciomyzidae).—Proceedings of the Entomological Society of Washington 81:285–297.
- . 1981. Revision of the Helosciomyzidae (Diptera).—Journal of the Royal Society of New Zealand 11(1):45–72.
- , & L. V. Knutson. 1989. 86. Family Sciomyzidae. Pp. 566–569 in N. Evenhuis, ed., Catalog of the Diptera of the Australasian and Oceanian Regions. B. P. Bishop Museum special publication 86 and E. J. Brill, Honolulu & Leiden, 1155 pp.
- Berg, C. O. 1953. Sciomyzid larvae that feed on snails.—Journal of Parasitology 39:630–636.
- , & L. V. Knutson. 1978. Biology and systematics of the Sciomyzidae.—Annual Review of Entomology 23:238–258.
- , B. A. Foote, & S. E. Neff. 1959. Evolution of predator-prey relationships in snail-killing sciomyzid larvae (Diptera).—Bulletin of the American Malacological Union Incorporated 25:10–13.
- Boyes J. W., L. V. Knutson, K. Y. Jan, & C. O. Berg. 1969. Cytotaxonomic studies of Sciomyzidae (Diptera: Acalyptrata).—Transactions of the American Microscopical Society 88:331–356.
- Bratt, A. D., L. V. Knutson, B. A. Foote, & C. O. Berg. 1969. Biology of *Pherbellia* (Diptera: Sciomyzidae).—Memoirs of the Cornell University Agricultural Experiment Station, New York State College of Agriculture 404:1–246.
- Brooks, D. R. 1989. Manual de metologia cladística. Rio de Janeiro, Academia Brasileira de Ciências, 109 pp.
- Carpenter, J. M. 1988. Choosing among multiple equally parsimonious cladograms.—Cladistics 4(3):291–296.
- Carvalho, C. J. B. de. 1989. Classificação de Muscidae (Diptera): uma proposta através da análise cladística.—Revista Brasileira de Zoologia 6(4): 627–648.
- Cresson, E. T., Jr. 1920. A revision of the Nearctic Sciomyzidae (Diptera, Acalyptratae).—Transactions of the American Entomological Society 46:27–89.
- Dietrich, C. H., & S. H. McKamey. 1995. Two new Neotropical treehopper genera and investigation of the phylogeny of the subfamily Membracinae (Homoptera: Membracidae).—Proceedings of the Entomological Society of Washington 97(1):1–16.
- Farris, J. S. 1988. Reference manual, Version 1.5. James S. Farris. 18 pp.
- Ferrar, P. 1987. A guide to the breeding habits and

- immature stages of Diptera Cyclorrhapha.—Entomograph 8(1-2):1-907.
- Fisher, T. W., & R. E. Orth. 1964. Biology and immature stages of *Antichaeta testacea* Melander (Diptera: Sciomyzidae).—Hilgardia 36:1-29.
- Foote, B. A. 1959. Biology and life history of the snail-killing flies belonging to the genus *Sciomyza* Fallén (Diptera, Sciomyzidae).—Annals of the Entomological Society of America 52(1): 31-43.
- , & L. V. Knutson. 1970. Clam-killing fly larvae.—Nature 226(5244):466.
- , S. E. Neff, & C. O. Berg. 1960. Biology and immature stages of *Atrichomelina pubera* (Diptera: Sciomyzidae).—Annals of the Entomological Society of America 53:192-199.
- Ghorpadé, K., L. Marinoni, & L. Knutson. 1999. *Steyskalina picta*, new genus and species of Tetanocerini (Diptera: Sciomyzidae) from the Oriental Region.—Revista Brasileira de Zoologia 16(3): 835-839.
- Griffiths, G. C. D. 1972. The phylogenetic classification of Diptera Cyclorrhapha, with special references to the structure of the male postabdomen. Series Entomologica 8. W. Junk, N.V., The Hague, 340 pp.
- Hendel, F. 1924. Die Paläarktischen Muscidae acalyptratae Girschn. = Haplostomata Frey nach ihren Familien und Gattungen. II. Die Gattungen.—Konowia [1923] 2(5-6):203-215.
- Kaczynski, V. W., J. Zuska, & C. O. Berg. 1969. Taxonomy, immature stages, and bionomics of the South American genera *Perilimnia* and *Shannonia* (Diptera: Sciomyzidae).—Annals of the Entomological Society of America 62:572-592.
- Knutson, L. V. 1966. Biology and immature stages of malacophagous flies: *Antichaeta analis*, *A. atriseta*, *A. brevipennis*, and *A. obliviosa* (Diptera: Sciomyzidae).—Transactions of the American Entomological Society 92:67-101.
- . 1970. Biology and immature stages of *Tetanura pallidiventris*, a parasitoid of terrestrial snails (Diptera: Sciomyzidae).—Entomologica Scandinavica 1:81-89.
- . 1972. Description of the female of *Pherbecta limenitis* Steyskal (Diptera: Sciomyzidae), with notes on biology, immature stages, and distribution.—Entomological News 83:15-21.
- . 1973. Biology and immature stages of *Coremacera marginata* F., a predator of terrestrial snails (Diptera: Sciomyzidae).—Entomologica Scandinavica 4(2):123-133.
- . 1976. Sciomyzidae flies: another approach to biological control of snail-borne diseases.—Insect World Digest 3(4):12-18.
- . 1987. Chapter 84. Sciomyzidae. Pp. 927-940 in J. F. McAlpine et al., eds., Manual of Nearctic Diptera, vol. 2. Agriculture Canada, Research Branch, Monograph 28, Ottawa, Pp. 675-1332.
- , & J. Abercrombie. 1977. Biology of *Antichaeta melanosoma* (Diptera: Sciomyzidae), with notes on parasitoid Braconidae and Ichneumonidae (Hymenoptera).—Proceedings of the Entomological Society of Washington 79: 111-125.
- , & C. O. Berg. 1963. Biology and immature stages of a snail-killing fly *Hydromya dorsalis* (Fabricius) (Diptera: Sciomyzidae).—Proceedings of the Royal Entomological Society of London 38(4-6):45-58.
- , & ———. 1964a. Biology and immature stages of malacophagous Diptera of the genus *Knutsonia* Verbeke (Sciomyzidae).—Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 43(7):1-60.
- , & ———. 1964b. Biology and immature stages of snail-killing flies: the genus *Elgiva* (Diptera: Sciomyzidae).—Annals of the Entomological Society of America 57:173-192.
- , & L. Lyneborg. 1965. Danish Acalyptratae flies. 3. Sciomyzidae (Diptera).—Entomologiske Meddelelse 34:61-101.
- , & K. Valley. 1978. Biology of a Neotropical snail-killing fly, *Sepedonea isthmi* (Diptera: Sciomyzidae).—Proceedings of the Entomological Society of Washington 80:197-209.
- , S. E. Neff, & C. O. Berg. 1967. Biology of snail-killing flies from Africa and Southern Spain (Sciomyzidae: *Sepedon*).—Parasitology 57:487-505.
- , R. E. Orth, & R. Rozkošný. 1990. New North American *Colobaea*, with a preliminary analysis of related genera (Diptera: Sciomyzidae).—Proceedings of the Entomological Society of Washington 92:483-492.
- , R. Rozkošný, & C. O. Berg. 1975. Biology and immature stages of *Pherbina* and *Psacadiina* (Diptera, Sciomyzidae).—Acta Scientiarum Naturalium Academiae Scientiarum Bohemoslovacae Brno (new series) 9(1):1-38.
- , E. R. Shahgudian, & G. H. Sahba. 1973. Notes on the biology of certain snail-killing flies (Sciomyzidae) from Khuzestan (Iran).—Iranian Journal of Public Health 2(3):145-155.
- , J. W. Stephenson, & C. O. Berg. 1965. Biology of a slug-killing fly, *Tetanocera elata* (Diptera: Sciomyzidae).—Proceedings of the Malacological Society of London 36:213-220.
- , ———, & ———. 1970. Biosystematic studies of *Salticella fasciata* (Meigen) a snail-killing fly (Diptera: Sciomyzidae).—Transactions of the Royal Entomological Society of London 122:81-100.
- Knutson, L. V., G. C. Steyskal, J. Zuska, & J. Abercrombie. 1976. Family Sciomyzidae. Pp. 1-24

- in N. Papavero, ed., A catalogue of the Diptera of the Americas south of the United States. São Paulo, Museu de Zoologia 64.
- Marinoni, L., & C. J. B. Carvalho. 1993. Cladistic analysis of *Protodictya* (Diptera, Sciomyzidae).—Proceedings of the Entomological Society of Washington 95:412–417.
- , & L. V. Knutson. 1992. Revisão do gênero Neotropical *Protodictya* Malloch, 1933 (Diptera, Sciomyzidae).—Revista Brasileira de Entomologia 36:25–45.
- McAlpine, J. F. 1989. Chapter 116. Phylogeny and classification of the Muscomorpha. Pp. 1397–1502 in J. F. McAlpine & D. M. Wood, eds., Manual of Nearctic Diptera, vol. 3. Agriculture Canada, Research Branch, Monograph 32, Ottawa, Pp. 1333–1581.
- Napp, D. S. 1994. Phylogenetic relationships among the subfamilies of Cerambycidae (Coleoptera, Chrysomeloidea).—Revista Brasileira de Entomologia 38:265–417.
- Neff, S. E., & C. O. Berg. 1961. Observations on the immature stages of *Protodictya hondurana* (Diptera Sciomyzidae).—Bulletin of the Brooklyn Entomological Society 56:46–56.
- , & ———. 1962. Biology and immature stages of *Hoplodictya spinicornis* and *H. setosa* (Diptera: Sciomyzidae).—Transactions of the American Entomological Society 88:77–93.
- , & ———. 1966. Biology and immature stages of malacophagous Diptera of the genus *Sepedon* (Sciomyzidae).—Bulletin of the Agriculture Experiment Station, Virginia Polytechnic Institute 566:1–113.
- Orth, R. E., & L. Knutson. 1987. Systematics of snail-killing flies of the genus *Elgiva* in North America and biology of *E. divisa* (Diptera: Sciomyzidae).—Annals of the Entomological Society of America 80(6):829–840, 17 figs.
- Pape, T. 1992. Phylogeny of the Tachinidae family-group (Diptera: Calyptratae).—Tijdschrift voor Entomologie 135:43–86.
- Rozkošný, R. 1987. A review of the Palaearctic Sciomyzidae (Diptera). Univerzita J. E. Purkyně v Brně. 101 pp.
- , & K. Elberg. 1984. Family Sciomyzidae. Pp. 167–193 in A. Soós & L. Papp, eds., Catalogue of the Palaearctic Diptera, vol. 3. Budapest, Hungary: Natural History Museum, 460 pp.
- , & L. V. Knutson. 1970. Taxonomy, biology, and immature stages of Palearctic *Pteromicra*, snail-killing Diptera (Sciomyzidae).—Annals of the Entomological Society of America 63:1434–1459.
- Steyskal, G. C. 1957. The postabdomen of male Acalyptrate Diptera.—Annals of the Entomological Society of America 50:66–73.
- . 1959. The American species of the genus *Tetanocera* Duméril (Diptera).—Papers of the Michigan Academy of Science Arts and Letters XLIV:55–91.
- . 1965. The subfamilies of Sciomyzidae of the world (Diptera: Acalyptratae).—Annals of the Entomological Society of America 58:593–594.
- . 1973. A new classification of the *Sepedon* group of the family Sciomyzidae (Diptera) with two new genera.—Entomological News 84(5):143–146.
- Tonnoir, A. L., & J. R. Malloch. 1928. New Zealand Acalyptratae. Part 4. Sciomyzidae.—Records of the Canterbury Museum 3(3):151–179.
- Vala, J. C. 1986. Description des stades larvaires et données sur la biologie de *Trypetoptera punctulata* (Diptera, Sciomyzidae).—Annales de la Société Entomologique de France (new series) 22(1):67–77.
- , & C. Caillet. 1985. Description des stades immatures et biologie de *Euthycera leclercqi* (Diptera, Sciomyzidae).—Revue Française d'Entomologie (new series) 7(1):19–26.
- , & C. Gasc. 1990. *Pherbina mediterranea*: immature stages, biology, phenology and distribution (Diptera: Sciomyzidae).—Journal of Natural History 24:441–451.
- , & L. V. Knutson. 1990. Stades immatures et biologie de *Limnia umquicornis* (Scopoli), diptère Sciomyzidae prédateur de mollusques.—Annales de la Société Entomologique de France 26:443–450.
- , P. T. Bailey, & C. Gasc. 1990. Immature stages of the fly *Pelidnoptera nigripennis* (Fabricius) (Diptera: Phaeomyiidae), a parasitoid of millipedes.—Systematic Entomology 15:391–399.
- , C. Caillet, & C. Gasc. 1987. Biology and immature stages of *Dichetophora obliterateda*, a snail killing fly (Diptera: Sciomyzidae).—Canadian Journal of Zoology 65:1675–1680.
- , J. M. Reidenbach, & C. Gasc. 1983. Biologie des stades larvaires d'*Euthycera cribrata* (Rondani 1868), parasitoïde de Gastéropodes terrestres. Première cycle expérimental une espèce du genre *Euthycera* Latreille 1829 (Diptera: Sciomyzidae).—Bulletin de la Société Entomologique de France 88:250–258.
- , G. Gbedjissi, L. Knutson, & C. Dossou. 2000. Not all sciomyzids kill mollusks, *Sepedonella nana* eats worms.—Science (in press).
- Valley, K., & C. O. Berg. 1977. Biology, immature stages, and new species of snail-killing Diptera of the genus *Dictya* (Sciomyzidae).—Search of Agricultural Entomology 7(2):1–45.
- Watrous, L. E., & Q. D. Wheeler. 1981. The out-group comparison method of character analysis.—Systematic Zoology 30(1):1–11.
- Wiley, E. O. 1981. Phylogenetics: the theory and prac-

tice of phylogenetic systematics. John Wiley and Sons, New York.

———, D. Siegel-Causey, D. R. Brooks, & V. A. Funk. 1991. The complete cladist: a primer of phylogenetic procedures. Special Publication 19, The University of Kansas, Museum of Natural History, Lawrence, Kansas, 158 pp.

Appendix 1.

List of genera and type species used in the analysis.

- Antichaeta analis* Meigen, 1830
Atrichomelina pubera (Loew), 1862
Calliscia calliscelles (Steyskal), 1963
Chasmacryptum seriatimpunctatum Becker, 1907
Colobaea bifasciella (Fallén), 1820
Coremacera marginata (Fabricius), 1775
Dichetophora obliterated (Fabricius), 1805
Dictya umbrarum (Linnaeus), 1758
Dictyacium ambiguum (Loew), 1864
Dictyodes dictyodes (Wiedemann), 1830
Ectinocera borealis Zetterstedt, 1838
Elgiva cucularia (Linnaeus), 1767
Ethiolimnia platalea Verbeke, 1950
Euthycera chaerophylli (Fabricius), 1798
Euthycerina vittithorax Malloch, 1933
Eutrichomelina fulvipennis (Walker), 1837
Guatemalaia straminata (Wulp), 1897
Hedria mixta Steyskal, 1954
Hoplodictya setosa (Coquillett), 1901
Hydromya dorsalis (Fabricius), 1775
Ilione albiseta (Scopoli), 1763
Limnia unguicornis (Scopoli), 1763
Neolimnia repo Barnes, 1976
Oidematops ferrugineus Cresson, 1920
Parectinocera neotropica Becker, 1919
Perilimnia albifacies Becker, 1919
Pherbecta limenitis Steyskal, 1956
Pherbellia punctata (Fabricius), 1791
Pherbina coryleti (Scopoli), 1763
Poecilographa decora (Loew), 1864
Protodictya chilensis Malloch, 1933
Pscadina disjecta Enderlein, 1939
Pteromicra glabricula (Fallén), 1820
Renocera pallida (Fallén), 1820
Salticella fasciata (Meigen), 1830
Sciomyza simplex Fallén, 1820
Sepedomerus macropus (Walker), 1849
Sepedon sphegea (Fabricius), 1775
Sepedonea lindneri (Hendel), 1932
Sepedonella nana Verbeke, 1950
Sepedoninus planifrons Verbeke, 1950
Shannonia meridionalis Zuska, 1969
Steyskalina picta Ghorpadé and Marinoni, 1999
Tetanocera elata (Fabricius), 1781
Tetanoceroides mesopleuralis Malloch, 1933
Tetanura pallidiventris Fallén, 1820
Teutoniomyia plaumanni Hennig, 1952
Thecomyia longicornis Perty, 1833
Trypetolimnia rossica Mayer, 1953
Trypetoptera punctulata (Scopoli), 1763